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THE EVOLUTION OF DOMINANCE IN CERTAIN POLYMORPHIC SPECIES

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1. SELECTIVE EQUILIBRIUM IN POLYMORPHIC SPECIES

IN his very interesting contribution to the problem of the evolution of dominance, published in the AMERICAN NATURALIST of January, 1930, Mr. J. B. S. Haldane calls attention to the peculiar dominance phenomena found by Nabours in the grouse locusts *Paratettix* and *Apotettix,* and by Winge in the fish *Lebistes reticulatus.* These, and I shall suggest that some of the land-snails such as *Helix hortensis* and *H. nemoralis* should be added to the list, have each of them three remarkable characteristics in common. The wild forms are all visibly polymorphic. The polymorphism may in each case be shown to be determined by genes or gene-complexes which are very closely linked in inheritance. Finally, each species has a relatively common "universal recessive," together with a number of usually less common dominant forms, which, if allelomorphic, show no mutual dominance, but have heterozygotes combining the characteristics of the two dominant homozygotes. The recessiveness of the "universal recessive," apart from rare deviations in some compound types produced in culture, seems to be complete.

Haldane had previously suggested with respect to the grouse locusts, and Demerec later with respect to *Lebis-*

tes, that the close linkage and frequent apparent allelomorphism observed in these groups was due not only to the infrequency of crossing over in their chromosomes, but to several chromosomes received from the same parent being generally transmitted in a group to the same offspring. Haldane now, with the support of C. D. Darlington and C. L. Huskins, has suggested that such linkage between chromosomes may be accounted for by sectional translocations, and that the dominant genotypes are themselves due to the duplication of such translocated segments. While some explanation of this kind appears to the writer extremely attractive in respect of the very close and frequent linkage observed, it is not so plain in what manner Haldane finds in it an explanation of the dominance phenomena. He says, "On the theory here adopted we need only suppose that some of the genes in the duplication have a greater effect when three or four are present than when only two are found, as in the normal type." This would indeed suffice to explain why the heterozygous duplication should differ from the universal recessive. But it gives no explanation of the completeness of dominance; it does not explain why the homozygous duplication should resemble the heterozygote. For this it is necessary to suppose, not only that some of the genes in the duplication have a greater effect when three are present, but also that none of them should exert a further effect when the three are increased to four; and this curious type of limitation must be observed in each of the possible duplications to which the different dominants are to be ascribed. Attractive as the suggestion is, therefore, in respect to linkage, it can not be regarded, as it stands, in any sense as an explanation of the dominance observed in these groups.

In previous papers (Fisher, 1928 *a* and *b*) I have developed a theory of the evolution of dominance by the natural selection of modifying factors, and have applied it to explain the generally observed recessiveness of deleterious mutants exposed to counter-selection, yet maintained at an extremely small frequency in the stock

by persistent mutation. Haldane seems to draw an analogy between such mutants and the less numerous genotypes of polymorphic species without sufficient circumspection. There is no good ground for regarding the less numerous genotypes of polymorphic species as subjected to counter-selection and only maintained in the stock by persistent mutation; indeed, the frequency with which they appear in nature would, unless the counter-selection postulated were exceedingly minute, require such enormous mutation rates as would inevitably have been detected in much less extensive experiments than those of Nabours and Winge. Mendelizing polymorphism may, on the contrary, be maintained indefinitely, as is probably the case with several polymorphic butterflies (Fisher, 1927), by a balance of selective actions, under which the frequency ratio of the contrasted genes settles down to a condition of equilibrium, which will be stable, to take the simplest case, if the heterozygote is at a selective advantage compared to both homozygotes. Since in the opposite case, when the heterozygote is the least advantageous phase, the equilibrium will be unstable and one or other homozygote must be exterminated, we should not expect to find such factors in nature. Stability, brought about by a favored heterozygote, may, on the contrary, be not uncommon, and there is some evidence in the case of the butterflies alluded to that the opposing selective forces consist on the one hand of the bionomic advantage of a mimetic or otherwise advantageous coloring, and on the other of some physiological factor such as inferior viability or fertility, associated with the dominant homozygote. Such cases appear to offer the unparalleled opportunity of estimating the magnitude of a bionomic advantage in nature by direct observation of the frequency of contrasted genotypes in the wild population, together with the experimental determination of the extent of inviability or sterility.

In this regard Nabour's genetical study of the grouse locusts has opened out a field of extraordinary interest. Haldane's remark, "Now on Fisher's theory there is no

obvious reason why modifiers should not be able to suppress the effect of a duplication as easily as that of a gene," may now be accepted in its full force, for there is no reason to suppose that the effects of the duplications, if duplications they are, have been exposed to counter-selection. Indeed, there are two reasons why the selection of dominance modifiers should be particularly effective in such cases. In the first place, the heterozygotes in which the effect of such modifiers is exposed to selection are now a perceptible percentage of the wild population, instead of having a frequency of the order of 1 in 10,000. This must increase the selective intensities about 100 or 1,000 fold, so that the difficulty felt by critics such as Wright and Haldane, who feel that in the case of deleterious mutations the selective intensities at work are too minute to have produced great results, is here removed. In the second place, if, as Haldane suggests, the dominant forms are due to a duplicated tract of chromatin, the evolutionary modification of this tract will take place almost wholly in heterozygous individuals. The selective advantage of any gene-contrasts within this tract will be totally unaffected by any reaction they might have produced in the "universal recessive," or in other dominant types. One may say that such a portion of chromatin is reserved for the evolutionary improvement of each particular heterozygote, and in less degree of the corresponding dominant homozygote.

Even without postulating duplication, a similar result will follow if, as is made probable by the high linkages observed, each dominant gene is situated in a section of chromatin in which crossing over never takes place. The evolutionary progress of such a section would then be wholly conditioned by the quality of its effects in the presence of the dominant gene. The modification of the extent of dominance through evolutionary changes in permanently associated genes bears some resemblance to Haldane's own views in depending on the selection rather of multiple allelomorphs than of multiple factors, for he has suggested that multiple allelomorphism is also re-

sponsible for the evolution of dominance against single defective gene mutations—an important suggestion, though made, I believe, for the wrong reason, for it is difficult to believe that the evolution will be hastened by throwing the whole burden on to one factor only out of the many thousands present, even though this one is clearly the most relevant.

The severest test of a theory is to build upon it a system of inferences, for if any rigorously logical inference is found to be untrue the theory fails. If, on the contrary, facts previously unsuspected are inferred from the theory, and found on trial to be true, the theory is undoubtedly strengthened. The plain inference from the theory of the modificatory selection of dominance and the fact that one particular pattern in the grouse locusts is recessive to all its natural alternatives is that this particular pattern is less advantageous than any of the others. This may seem surprising since this particular pattern is often, perhaps always, the most numerous in nature. We have, however, inferred only one half of the selective balance. The selective advantage of the heterozygote over the homozygous recessive is inferred from the fact of dominance to be due to its pattern. If there is a balance of selective agencies, the heterozygote must also enjoy some advantage over the homozygous dominant. In this contrast the patterns are alike, and we should naturally look for some constitutional difference affecting viability or fertility. Such a constitutional deficiency again accords well with the theory that we have to do with a homozygous duplication. It is of more direct consequence to our argument that a deficiency of homozygous dominants of sufficient magnitude to be statistically significant appears from the published record of Nabour's breeding experiments.

2. Viability of Homozygotes

In order to examine the evidence as to the viability of homozygotes, an exhaustive examination was made of the

very large body of data reported by Nabours in his experiments with *Apotettix* (Nabours, 1925).

Matings from which homozygotes of the dominant forms appear are necessarily unsuitable for studies of linkage. Only a minority of Nabour's experiments can therefore be available for studying their viability. In matings of the generalized type P/Q × P/Q homozygotes and heterozygotes should appear in equal numbers, or, strictly, in proportion to their viability up to the time of classification. A comparison between the observed frequencies in such matings should, therefore, if the material proves to be sufficiently ample, supply an indication of any existing difference in viability. These matings will, however, show a certain small proportion of recombined types, some of which are not phenotypically separable from the three main types of offspring, and although the frequency of recombination is small, it is important that the treatment of the recombined types should allow of no bias in the massed comparisons.

Of the four recombined types which should appear in equal numbers two, namely, P/+ and Q/+, will have been classified as homozygotes, while the remaining two, P/PQ and Q/PQ, will generally have been classed as heterozygotes; exceptionally, as with the mating Y/T × Y/T, these latter classes are recorded separately, and in such cases they have been added to the heterozygotes. If viability is equal, crossing over thus introduces no bias into the main comparison, though by classifying a small proportion of homozygotes as heterozygotes and an equal proportion of heterozygotes as homozygotes the effect sought for will certainly be diluted.

If p is the recombination fraction, and $q = 1 - p$, the viability (v) as determined from the frequency ratio of the offspring as classified will be related to the true viability v_o, by the equations

$$v = \frac{qv_o + p}{q + pv_o}, \qquad v_o = \frac{qv - p}{q - pv},$$

which may be used to correct the estimates obtained. Such corrections can not, of course, influence the test of significance.

Many of the matings are, however, of the type PQ/R × PQ/R. In addition to the possible recombination of PQ and R, we have here also the two additional types of recombination involving the separation of P from Q. Thus the recombined gametes P and QR will yield zygotes PQ/P and PQ/QR which will be classified as PQ/PQ and PQ/R, respectively, together with two independently classified zygotes R/P and R/QR. Bias may in this case be avoided by classing these with R/PQ and R/R, respectively, and the same convention is applied in the classification of the recombined zygotes R/Q and R/PR, whenever they occur. In this case also there will be some dilution of the effect sought for, but its test of significance is unaffected.

Table I gives the frequencies for the forty types of mating available, the reference numbers in the first column giving the first mating of each type. The crossovers capable of separate classification are in each case shown on a separate line, in the column to which they have been assigned. In the aggregate 4,309 homozygotes and 4,617 heterozygotes survived to be classified. This is a very considerable defect of homozygotes, not to be ascribed to chance, since it exceeds three times its standard error. The massed data demonstrate an appreciable defect of homozygotes. The percentage viability is about 92.9 per cent. of that of the heterozygotes.

In respect of individual dominants the data are necessarily less ample, though here also there are some cases which must be judged to be individually significant, and in all these the deficient class is that of the homozygotes. Table II shows the aggregate of homozygotes and heterozygotes for each dominant or compound of dominants tested. The dominants Y, O and R and the compounds RK, YK and MR all show individually significant deficiencies, while M, T, G, Z, YT and YZ all show deficiency in less degree. The cases of RK and YK are especially

TABLE I

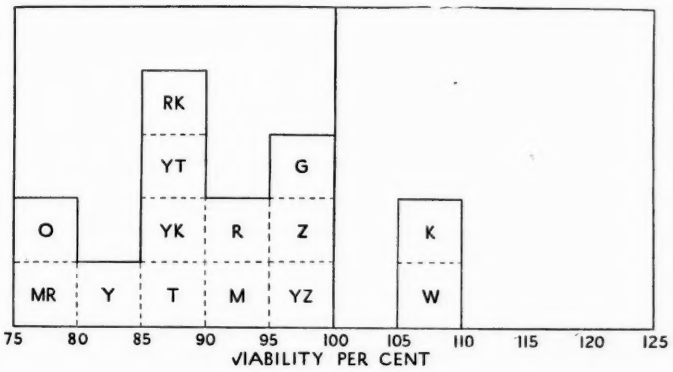
MATINGS OF TYPE P/Q × P/Q

Mating	Parents	Homozygotes	Heterozygotes	Homozygotes	Crossovers
370	H/G	15	28	15	
375	M/R	49	115	54	
391	M/W	27	47	26	
397	M/T	58	95	54	
399	M/G	76	147	83	
405	M/K	238	556	292	
422	Y/O	9	26	9	
431	Y/R	65	185	86	
439	Y/Z	71	145	72	
447	Y/T	12	48	22	
452	YT/O	14	42	14	
458	Y/K	33	69	37	
470	O/R	16	46	30	
471	O/T	18	24	14	
474	O/G	40	105	51	
482	O/K	8	28	8	
487	R/T	35	90	32	
492	R/K	88	168	100	
510	W/K	74	138	75	
517	Z/K	20	35	13	
524	Z/T	25	35	15	
525	T/G	32	62	27	
528	T/K	40	64	35	
541	MR/K	69	181	110	5
			2	3	
553	M/RK	85	167	73	
569	YZ/T	49	85	25	6
			5	1	
571	YZ/G	138	258	110	8
			4	4	
577	YZ/K	96	192	103	13
			8	5	
584	YT/R	134	312	149	1
			—	1	
605	YK/O	21	48	22	
612	YK/R	184	423	158	8
			4	4	
623	YK/Z	18	43	9	
624	YK/T	51	108	48	8
			7	1	
627	YT/K	29	35	20	9
			6	3	
631	RK/T	142	315	138	1
			—	1	
635	B/MRK	—	1	—	
636	MRK/T	5	20	4	
640	YK/RK	—	9	4	
641	YRK/G	8	7	5	3
			2	1	
643	YZ/RK	27	77	24	
	Total	2,119	4,617	2,190	

TABLE II

Factor	Homozygotes	Heterozygotes	Estimated viability per cent.
Dominants showing significant deficiency			
Y	190	473	80.3
O	127	319	79.6
R	605	1343	90.1
RK	243	568	85.6
YK	274	642	85.4
MR	69	183	75.4
Dominants showing non-significant deficiency			
M	533	1127	94.6
T	427	958	89.1
G	296	613	96.6
Z	126	258	97.6
B	0	1	—
YT	177	395	89.6
YZ	310	629	98.6
MRK	5	21	—
Dominants showing non-significant excess			
K	804	1482	108.5
W	100	185	108.1
H	15	28	—
YRK	8	9	—
Total	4309	9234	93.3

interesting, since K is the only dominant for which substantial data are available which by itself shows no deficiency of homozygotes. The only other cases of excess



are shown by W with only 285 observations, by H with only 43 and by YRK with only 17.

Fig. 1 shows the distribution of the fourteen viabilities, based each on over 200 survivors. The true viabilities will, as has been seen, be generally somewhat lower than those shown, which have not been corrected for dilution due to recombination.

The deliberate experimental determination of the selective viabilities of different homozygous and heterozygous types would evidently be of great value in clearing up the situation. In particular, though, on the view suggested, there is no reason to anticipate that the viability of the homozygous recessives should be inferior to that of the heterozygotes, there is some, though still inconclusive, evidence from Nabour's matings that this homozygote also may be at a slight disadvantage. Four types of matings are available on this point.

(i) When homozygous recessives (+/+) are mated with heterozygotes (+/Q) where Q stands for a dominant or compound of dominants, homozygotes and heterozygotes are expected in equal numbers. In this case all crossovers in the dominant compound are recognizable, and may be omitted. These matings are shown in Table III.

TABLE III. +/+×+/Q

Mating	+/+	+/Q
4	20	8
5	3	6
6	33	32
351	6	9
721	31	36
Total	93	91

This group gives 93 homozygous recessives to 91 heterozygotes, and shows no defect of homozygotes.

(ii) When like heterozygotes (+/Q) are interbred, a quarter homozygous recessives are expected, but the homozygous dominants can not be distinguished from the heterozygotes; only two of the four crossover classes are

distinguishable, the other two being confounded with the heterozygote and homozygous dominants. We may therefore subtract the number distinguishable from the number in this class. These matings are shown in Table IV.

TABLE IV. +/Q×+/Q

Mating	+/+	Q	Crossovers
287	77	114	—
292	2	10	—
312	4	12	—
316	5	24	—
348	5	16	—
352	28	82	—
365	24	81	—
443	14	52	4
469	32	118	11
521	26	91	—
1246	4	11	1
	221	611	16
		16	
		595	

This group gives 221 recessives to 595 heterozygous and homozygous dominants, and shows an appreciable excess of recessives. This is due, however, principally to the great excess shown in mating 287, which the other matings as a whole tend partially to counterbalance.

(iii) When heterozygotes +/P, +/Q are mated, the expectation is again a quarter recessives. If P and Q are compounds containing no dominant in common all the non-recessives will be heterozygotes, and all crossovers will be theoretically capable of detection. Those detected have therefore been omitted; Table V shows eighty-six types of mating of this class.

These give in all 1,732 recessives to 5,466 heterozygotes, a deficiency of recessives which only just falls short of twice the standard error. It is the material in Table V which makes it worth while to call attention to the possibility of making more direct tests of the viability of the recessive type, for though the data as they stand can not

TABLE V. +/P×+/Q

Mating	+/+	Heterozygous	Mating	+/+	Heterozygous	Mating	+/+	Heterozygous
275	5	21	755	38	118	1085	11	55
277	22	103	757	36	142	1099	27	55
282	15	63	837	2	6	1103	1	1
283	11	54	842	16	93	1104	1	13
285	43	102	843	104	332	1106	8	33
291	13	38	858	29	83	1113	28	87
293	13	46	860	0	8	1114	44	143
294	5	27	866	6	26	1115	34	75
295	26	73	868	10	21	1118	41	102
303	36	119	889	15	38	1160	50	159
311	24	62	890	12	25	1163	22	67
314	8	24	901	7	27	1164	90	241
315	0	5	990	0	1	1210	0	29
324	1	11	1011	13	74	1221	45	121
333	5	19	1013	8	37	1234	15	53
338	11	42	1015	3	11	1236	6	34
341	13	33	1017	10	29	1247	12	37
346	68	234	1030	2	14	1248	25	39
349	16	41	1031	35	155	1270	5	23
353	5	17	1032	14	58	1273	22	58
354	24	64	1033	25	62	1281	13	50
647	25	84	1054	56	157	1282	29	105
649	40	141	1055	1	2	1285	0	2
653	25	71	1056	27	61	1290	17	41
674	2	15	1066	17	75	1292	88	264
691	5	8	1068	1	10	1376	51	162
709	12	37	1072	7	15			
711	3	5	1082	53	114			
734	1	3	1083	4	2	Subtotal	685	2049
748	16	56	1084	3	3			
Subtotal	493	1618	Subtotal	554	1799	Total	1732	5466

be judged as showing a significant deficiency of recessives, they do raise the question whether there is not in reality such a deficiency, either of slight extent, or even possibly as great as has been found for some of the homozygote dominants.

(iv) A group of matings of type +/PR×+/QR produce not only a recognizable quarter of recessives, but also homozygotes in R distinguishable from the heterozygotes. In respect of crossing over between Q and R, two of the crossover classes will appear among the heterozygotes and dominant homozygotes respectively, while

the two other classes are recognizable. We therefore subtract half the observed crossovers from each of these two classes; other types of crossovers are recognized and may be ignored. Table VI gives the matings of this group.

TABLE VI

MATINGS OF TYPE +/PR × +/QR

Mating	+/+	Heterozygous	Homozygous	Crossovers
366	14	25	11	–
390	11	35	13	–
1069	3	7	2	–
1117	68	146	71	–
1119	21	61	25	6
	117	274	122	6
		3	3	
		271	119	

In this group the recessive homozygotes show a deficiency even greater than that shown by the dominant homozygotes; the data, are, however, quite insufficient to stand alone. They may, by throwing heterozygous and homozygous dominants together, be combined with Table IV showing together just such a slight excess of reces-

Table IV	221	595
Table VI	117	390
	338	985

sives as might be ascribable to the lower viability of the homozygous dominants, though the ratios are too heterogeneous for such an interpretation to be relied on. Finally we may throw together all the evidence on homozygous recessives by calculating from each table the expectation, based where possible on the heterozygotes observed.

The deficiency of eighty-four in all is, of course, not significant, though it may well be that the homozygous recessives are really less viable than the heterozygotes to the extent of about 3 or 4 per cent.

TABLE VII
SUMMARY FOR RECESSIVES

	Expected	Observed
Table III	91	93
Table IV	198	221
Table V	1,822	1,732
Table VI	136	117
Total	2,247	2,163

The finding of inferior viability among the homozygous dominants in *Apotettix* supports the view that the dominant patterns are in nature advantageous, not only by verifying a previously unsuspected fact deduced from this view, but by opening out the possibility of the direct experimental determination of the magnitude of the selective advantage of one color pattern over another in nature. For if a, b and c are proportional to the numbers of offspring left, on the average, by homozygous recessives, heterozygotes and homozygous dominants, respectively, then the ratio of recessive to dominant gametes will tend to approach the equilibrium value $(b - c)/(b - a)$. If therefore we are given the frequency of the different types in the natural population and can also determine experimentally the relative viabilities, and if necessary, also the fertilities in culture, we shall be in a position to infer the existence, and if our data are sufficiently accurate, to calculate the magnitude, of any selective advantage not due to constitutional causes, which in nature favors the dominants over the recessive. With increasingly precise data upon these points therefore it should be possible to put this interpretation of the dominance phenomena in the grouse locusts to a quantitative test.

3. *LEBISTES*

The condition found by Winge (1927) in *Lebistes reticulatus,* while showing some striking similarities, also differs in two important respects from that found in the grouse locusts. These are, first, that, with one excep-

tion, the genes found are sex-linked in inheritance; and secondly, that, with the exception of the autosomal gene in its homozygous condition, they are without visible effects in the female (save in certain females of intersexual character). In this fish the male is the heterogametic sex, so that without the transference of genes by crossing over from the X to the Y chromosome, or *vice versa,* it would be impossible to observe the phenomena of dominance in the sex-linked factors. Such transference has, however, been observed in several cases and, when the same factor is introduced into a male, both in its X and its Y chromosome, the fish is somatically like one into which it is introduced from one side or the other only. As far as is known, therefore, the sex-linked genes for color variants in the male may be said to be dominant, although it should be observed that Haldane's statement that "Winge found eighteen genes dominant to the normal and none recessive" is an induction from the cases so far observed, rather than a directly observed fact. The autosomal gene is also dominant in the male though it should be more properly described as recessive in the female, since it is only in the homozygous female that the striping (*zebrinus*) has been yet observed.

Dr. Winge informs me that the males are certainly polymorphic in nature, though the types obtainable from dealers are often more "beautiful" than those which can be found wild, thus suggesting that appreciable modification and gene combination have been brought about by human selection. His observations suggest the important conclusion that the X chromosome is usually "empty" (*i.e.,* the universal recessive), in wild specimens, and that the genes for additional color patterns in the males are, in nature, more fully confined to the Y chromosome than is the case in the domesticated breeds.

We have here a group of facts extremely suggestive of the interpretation, which we should at once infer from the view that dominance has been determined by selective agencies, namely, that the color variants are advantageous in the male and disadvantageous in the female.

Given the fundamental conditions for the stability of gene ratio, upon which any permanent Mendelizing polymorphism must rest, such a situation will lead, on our view, to consequences remarkably consonant with the facts observed. First, the variant form should become dominant in the male and recessive in the female fish; next, continued counter-selection in the female should obliterate entirely, in this sex, the effects of those genes which were capable of leaking into the X chromosome; thirdly, favorable selection in the males with counter-selection in the females should make the variants rarer in nature in the X chromosome than in the Y, although, in the absence of selection, crossing over should tend to equalize the proportions; fourthly, favorable selection in the Y chromosome, with counter-selection in the X, must constantly favor those genotypes in which linkage with the sex-determining portion of the Y chromosome is closest, and may thus have built up the system of close sex-linkage which is now found; fifthly, close linkage with Y may have enabled certain variants, beneficial in the male, to have established genetic stability, which, had they been autosomal, would have been definitely deleterious, and have never contributed to the natural polymorphism. It may be a coincidence that the one variant whose effect has not been entirely suppressed in the female is the only one that still stands outside the sex-linked system; even without unduly stressing this fact, however, it is difficult to imagine how the observed facts in *Lebistes* could more closely simulate those to be anticipated on the theory of the selective modification of dominance.

4. *HELIX*

The facts so far available as to polymorphism in the land snails, for which *Helix hortensis* and *nemoralis* may be taken as typical, seem closely to resemble those in the grouse locusts. A great variety of distinct forms exists in nature, and of these one of very general occurrence, and frequently the commonest, appears to be a universal

recessive. Captain Diver (1929) has ascertained that various forms now found appear without perceptible change in the proportions among Pleistocene remains, and we may somewhat confidently infer from this a definite mechanism of stability in the gene-ratios. Breeding experiments, of which few unfortunately have yet been published, appear to show, so far, complete linkage between the different factors, although types which may have arisen originally by recombination are found in nature.

Thus we find the three peculiar features, of polymorphism, close linkage and the universal recessive type of dominance, occurring together in groups as widely separated as are mollusks, vertebrates and insects, and we can scarcely doubt that the three phenomena are associated causally. While it is at present certainly premature to choose one of these three as the primary cause responsible for the other two, it is perhaps worth while, even now, to consider, in a spirit of conjecture, whether the close linkage may not, at least in the snails and grouse locusts, have played the primary rôle.

5. Evolutionary Conditions Induced by Close Linkage

Close linkage within and especially between chromosomes introduces one difficulty to normal evolutionary development which has not, I think, been recognized. While its ultimate discussion will undoubtedly require a far more refined mathematical development than I can here attempt, it does seem possible to gain a crude qualitative notion of its nature by considering the extreme, and perhaps unreal, case of a species in which no recombination whatever is possible. Any considerable change, in the evolution of a species from its ancestral form at a remote geological period, must have involved numerous genetic substitutions. The genetic novelties ultimately adopted must, as far as we know, have originated in mutations, though where free recombination is possible, we need by no means confine ourselves to the supposition that such mutations must necessarily have been bene-

ficial from their first appearance. It is indeed certain that many species contain a large amount of latent variability by the selection of which their instantaneous rates of evolutionary improvement are maintained. There is no need, however, to suppose that the whole of this is due to a stream of mutations beneficial from their first appearance, in process of spreading over the species, rather than that much of it may be due to effectively neutral mutations which have occurred in the past, and the ultimate fate of which is at present in process of decision. However this may be, in a species entirely devoid of recombination, and possessing for genetic purposes only a single gene, a beneficial substitution which could be adopted without hindrance, in a species enjoying the advantage of free recombination, will be threatened by every other genetic substitution possible within the genetic variance of the species, and will inevitably be pushed aside and suppressed if any such alternative substitution offers a greater selective advantage. The different genotypes will, in fact, compete with one another like a system of multiple allelomorphs, and instead of genetic improvement being possible simultaneously in hundreds of different loci, the steps of evolutionary improvement will have to take place one at a time, the weaker always making way for the stronger.

The chance of any particular substitution being adopted may be crudely represented as the chance that during a certain time, during which it is spreading through the species, no substitution more suitable than itself makes its appearance. If we represent by a the selective advantage of a substitution and by $\mu_a da$ the frequency with which substitutions in the range da present themselves, the time needed for the substitution to spread, within any assigned limits, over the population will be inversely proportional to a, while the frequency with which substitutions superior to any given level b appear will be represented by

$$\int_b^\infty \mu_a da$$

where μ_a doubtless falls off rapidly as a is increased. Consequently if b represents a level of advantage which has a tolerable chance of survival, before some bigger advantage can thrust it aside, we shall have some such relation as

$$bc = \int_b^\infty \mu_a da$$

where c is a constant, dependent from the chance of survival chosen. For a suitably chosen constant, b may be regarded as a standard level of selective advantage such that substitutions giving a selective advantage greater than b can and do prevail over their competitors, and so contribute to evolutionary progress, while those conferring a much smaller selective advantage have scarcely any chance of doing so. There will, in fact, in such cases be something like a real *limen* of selective advantage, such as Sewall Wright has suggested even for cases involving free recombination. It is not unreasonable to suspect that the chance of success for selective advantages less than b may be proportional to $e^{-b/a}$, an expression that diminishes with extreme rapidity as a is diminished, although when a is so small that the expression approaches $1/(2n)$, where n is the number of parents breeding in each generation, the probability must remain nearly constant until a falls to zero.

For the more practical case, in which some degree of recombination is possible, the state of affairs appears at first sight to be similar, though with a larger value of the constant c, which may be expected to increase with increasing recombination, in proportion to the number of separable loci in the species; and, unsatisfactory as such a crude approach must be felt to be, it does seem to show with sufficient clarity that when linkage is, as with the species here considered, extremely close, it will be impossible to utilize a number of the smaller genetic improve-

ments which present themselves, because the whole of the existing nuclear material is fully occupied with matters of more importance.

Now the system of obtaining improved color patterns, such as appears to fit the facts with the grouse locusts, by dominant duplications, which are deleterious in the homozygous phase, at once raises the problem of why the universal recessive can not itself be modified to a more advantageous pattern, and so supersede the dominants with which it appears to be now in equilibrium. There is little harm in putting forward a conjecture so long as it is clearly recognized as such, and it appears to the writer possible that the color pattern of the grouse locust is not among the more important matters with which its evolutionary progress is urgently concerned. What these more important matters are it would be idle to guess—perhaps its digestion or its vision or its reproductive instincts may be of greater real importance to the insect; at least we can not fairly assume that the real importance of a feature is in any way measured by its conspicuousness to ourselves, and we have no reason at present to assume without question that the universal recessive, in species with such close linkage as the grouse locusts, is free to seize upon any such relatively trifling advantage as might be gained by modifying its color pattern.

This point of view brings out, I think, one of the most attractive features of the theory of duplications, for if modifications in color pattern are too unimportant to win their way to success in the germ-plasm of the universal recessive, it is clear that modifications of the heterozygote must be due to factors located elsewhere, and the theory supplies a tract of chromatin where such factors, though they may compete among themselves, are protected from outside competition. On this view the evolution of dominance would have taken place by the selective modification of the duplication itself. The same of course could be said, without duplication, of any tract permanently associated with the dominant gene.

6. Summary

Polymorphism in wild populations must usually imply a balance of selective agencies, of which the simplest type is a selective advantage of the heterozygote over both homozygotes. Such a condition should not be confused with the maintenance of a rare mutant type against counter-selection by means of repeated mutations. While such mutations should on the theory of the selective modification of dominance tend to become recessive, heterozygotes in polymorphic species will tend to resemble in external appearance whichever homozygote it is most advantageous to resemble. The selective balance must then be maintained by some constitutional disadvantage of the homozygous dominant.

The modification of dominance should in such cases be especially rapid; partly by reason of the far greater frequencies of the heterozygotes exposed to selection, and partly, if any tract of chromatin is permanently associated with the dominant gene, from the fact that the evolutionary modification of such a tract will be reserved for the improvement of the heterozygote, and in less degree of the corresponding homozygote.

Nabours' experiments with the grouse locust *Apotettix* do, in fact, show such a deficiency of homozygous dominants as is required by this theory. The average amount of the deficiency is about 7 per cent. In six individual cases the deficiency is statistically significant, and six more show a non-significant deficiency, against two showing a non-significant excess.

It is not certain from the existing data whether the homozygous recessive is equivalent in viability to the heterozygotes, or suffers also from a slight defect in viability. Deliberate experiments on the viability of the different genotypes together with counts of the frequencies in nature would enable the inference that the dominants really exhibit the more advantageous patterns to be put to a quantitative test.

The incidence of dominance and linkage in the fish *Lebistes reticulatus* strongly suggests that the colored genes

found by Winge are advantageous in the male but disadvantageous in the female.

The association of the three peculiarities of polymorphism, close linkage and the universal recessive type of dominance is found in mollusks, arthropods and vertebrates. It is tentatively suggested that, at least in the grouse locusts and the snails, the primary cause of the two other phenomena may be found in the closeness of linkage within or between chromosomes. This condition presents an obstacle to normal evolutionary development by gene substitution, and so makes it possible for abnormalities such as duplications to possess occasional advantages, so setting up the stability of the gene-ratio necessary for polymorphism; if the advantage lies in the external appearance, the polymorphism will be manifest, and the variant form will tend to become dominant.

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CAUSES OF DIFFERENCE IN SUCCESS OF RECIPROCAL INTERSPECIFIC CROSSES

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IN crossing distinct species the degree of success depends in many cases on the direction in which the cross is made. One of a pair of reciprocal crosses may present little difficulty while the other always ends in failure; one may be easy to make and the other difficult; both may be difficult but one distinctly harder than the other; there may be only a slight difference in the number or quality of the seeds formed. In all such cases the difference in question is in respect to the formation of crossed seed which can grow into F_1 plants; once the hybrids are produced, with very rare exceptions they are found to be identical in fertility as well as in other characteristics. In what follows, the expression "difference between reciprocal crosses" refers only to this difference in success or difficulty.

The causes of such differences are unknown in all but a few instances. A difference between the parents with respect to the length of the style is thought to be the important factor in some cases. Focke (1881) stated that *Mirabilis jalapa* can be crossed with *M. longiflora* if the former is used as the female parent but not if it is used as the male. Strasburger (1886) and Jost (1907) showed that though the pollen grains of each germinate equally well on the stigmas of the other, the tubes of *jalapa* are unable to make their way completely through the long styles of *longiflora* whereas the tubes of *longiflora* easily traverse the short styles of *jalapa*. The same cause has recently been suggested by Ostenfeld (1929) for his repeated failures in crossing *Polemonium pauciflorum* ♀ with *P. mexicanum* ♂ and his success in the reciprocal. The style of *pauciflorum* is about eight times as long as

that of *mexicanum*. There are numerous cases, however, in which the styles of the two species are of similar length and in which this explanation is consequently out of the question. In view of the great variety of materials it is not probable that the cause is always the same.

It is possible that in some cases the pollen tubes of one species may be injured in the stigma of the other. Bucholz and Blakeslee (1929) reported that the tubes of tetraploid *Datura* grow quite abnormally and usually burst in the stigmas of diploids, so that the cross in this direction is quite unsuccessful. In the reciprocal the growth of the tubes is normal and the cross successful. This phenomenon has not been observed in species crosses, so far as I am aware.

It is also possible that in some cases the explanation may be similar to that which was advocated by Correns (1928) to account for the very rare cases in which reciprocal hybrids differ in certain characteristics. The assumption is that the cytoplasm of one parent lacks the proper materials (or enough of them) to enable certain genes of the other to produce their normal characters. Similarly it is conceivable that the cytoplasm of one may lack materials which are necessary for development to occur at all when the genes are from the other parent. At any rate some peculiar interaction (or failure to interact) between the genes of one parent and the cytoplasm of the other may be responsible for cases of difference in success of reciprocal crosses. In many cases, however, cross fertilization is accomplished and seeds are formed but whereas in one cross the seeds are normal, in the reciprocal they are shriveled and germinate badly.

Another cause, which can be clearly demonstrated, operates in species crosses in wheat, as shown by Watkins (1927) and by Thompson and Cameron (1928). In crosses between twenty-one-chromosome species (*vulgare* series) and those with fourteen (emmer series) the F_1 grains are plump when the twenty-one-chromosome par-

ent is female and wrinkled when it is male. In the former case the endosperm is diploid for the extra seven chromosomes which *vulgare* possesses and emmer lacks, and in the latter case it is haploid. This difference depends on the fact that the female parent contributes two nuclei to the endosperm and the male only one. The plump grains of the 21 x 14 cross germinate much better than the wrinkled ones of 14 x 21. Thompson (1930) investigated the relation between chromosome conditions and shriveled endosperm in many types of backcrosses and F_2 and concluded that the endosperm is well developed whenever it is diploid or triploid for the whole set of extra seven *vulgare* chromosomes (or has none of them as in pure emmer) and is wrinkled when haploid for them and particularly when incomplete sets are doubled or tripled.

Differences in the difficulty of making other reciprocal wide crosses in wheat seem to depend on the same principle. (*a*) Species of the emmer group ($n = 14$) can be readily crossed with *Triticum monococcum* ($n = 7$) when they are female, but the reciprocal crosses present greater difficulty. In the former case the set of seven chromosomes which the emmers possess and which *monococcum* lacks is diploid in the endosperm, and the latter haploid. (*b*) The cross between twenty-one- and seven-chromosome wheats is difficult in either direction but distinctly easier when the species with the larger number is used as female. (*c*) With one exception all the numerous investigators of the cross between *vulgare* and rye ($n = 7$) have found it necessary to use the wheat as the female parent, the reciprocal cross proving unsuccessful. Meister and Tjumjakoff (1928) alone have reported some success in crossing rye ♀ with wheat ♂ but only about 2 per cent. of their pollinated flowers set seed, whereas in the reciprocal the percentage was more than 60. (*d*) Similar results have been obtained in crossing emmer wheat with rye. (*e*) Emmer ♀ x *Aegilops spel-*

toides ♂ (n = 7) is possible though difficult, but the reciprocal has invariably proved unsuccessful in many trials. In all these cases the best results are obtained when the parent with the larger chromosome number is female. Leighty, Sando and Taylor (1926) have reported crosses between twenty-one-chromosome wheats and fourteen-chromosome *Aegilops* in which more grains were obtained when the *Aegilops* was female but they also stated that the differences were not significant because all the *Aegilops* flowers were receptive at the same time while those of wheat were not (particularly since they used eighteen to twenty-four flowers per ear).

The reason for the greater success when the female has the larger chromosome number is that then the chromosomes by which the parents are distinguished are doubled in the endosperm while in the reciprocal they are single. The difference probably depends not only on the mere fact that the excess chromosomes are in the 2n condition in the one and the n condition in the other but also on the fact that they are genetically distinct from those in the 3n condition.

It seemed worth while to determine whether the rule which holds in interspecific crosses in wheat would hold in other plants. It is true that the endosperm is more abundant in the seeds of cereals than in those of most other plants, but even in those cases in which there is little endosperm in mature seeds it has usually played an important part at earlier stages, being used up during the development of the embryo (Coulter and Chamberlain, 1912). A search of the literature was therefore made to discover whether the relationship was of general occurrence.

The genus *Nicotiana* furnishes much evidence in point, for many of its species which have different chromosome numbers have been crossed in various combinations and in many cases reciprocal crossings have yielded different results. The data given in Table I have been taken

TABLE I

RESULTS OF RECIPROCAL CROSSES BETWEEN SPECIES OF *Nicotiana* (DATA FROM EAST, 1928)

	alata 9	Langsdorffii 9	Sanderae 9	longiflora 10	plumb. 10	acuminata 12	glauca 12	glutinosa 12	paniculata 12	sylvestris 12	trigonophylla 12	suaveolens 16
longiflora 10 ♀	+	−	+									
♂	+	−										
plumbaginafolia 10 ♀	+	+	−									
♂	−	−										
acuminata 12 ♀	+	−	−	+	+							
♂	−	−	−	−	−							
glauca 12 ♀	+	+	+									
♂		−										
glutinosa 12 ♀	−	+	−	−	−							
♂	−	−		−	−							
paniculata 12 ♀	+	+	+	+	+							
♂	+	−		−	−							
sylvestris 12 ♀	−	−	−	−	−							
♂	−	−	−	−	−							
trigonophylla 12 ♀	−	+	−	−	−							
♂	−	−		−	−							
suaveolens 16 ♀	+	+	+	+	+	+		+	+	−	−	
♂	−	−	−	−	−	−		+	+	−	−	
Bigelovii 24 ♀	−	+	−	+	+	−		+	+	+	−	+
♂	−	+	−	−	−	−	−	+	+	−	−	+
nudicaulis 24 ♀	−	−					+		−		+	−
♂	−	−					−	+	−		−	−
rustica 24 ♀	+	+	+	−	−	−		+	+		−	+
♂	−	−	−	−	−	−	−	−	+	−	−	−
Tabacum 24 ♀	+	+	+	+	+	+	+	+	+	+	−	−
♂	+	−	−	−	+	−	+	+	+	+	−	+

from East's (1928) summary of the work of numerous investigators. It includes the reported results of all reciprocal crosses between species of *Nicotiana* which differ in chromosome number, except those involving *Rusbyi* and *tomentosa* in which there were no cases of difference between reciprocals. The haploid chromosome number is given in connection with each specific name and the table is arranged so that for any one cross

the species with the larger chromosome number is in the horizontal line and that with the smaller in the vertical line. The + sign indicates that the cross has been successfully made; the — indicates that it failed, usually at the hands of several investigators. The significant point in this table is that with one exception wherever the signs for a pair of reciprocal crosses differ the + occurs opposite the ♀; that is, the cross was successful when the female parent had the larger chromosome number. There are thirty-one cases represented in this table in which one of a pair of reciprocal crosses proved successful and the other unsuccessful; in thirty of them the successful one was that in which the female parent had the larger chromosome number. The principle which was worked out in wheat therefore appears to hold in the numerous crosses in *Nicotiana.*

There is additional evidence in connection with *Nicotiana* which does not appear in the table. In several cases although reciprocal crosses are represented by the same sign they really differ in difficulty. For example, *longiflora* ♀ x *alata* ♂ is easier than the reciprocal. *Rustica* (24) ♀ x *paniculata* (12) ♂ is much easier than the reciprocal because the seeds of the latter are shriveled and germinate badly. *N. digluta* which originated from the hybrid *glutinosa* x *tabacum* through doubling of the chromosomes (Clausen and Goodspeed, 1925) crosses readily with both *glutinosa* and *tabacum* when it is used as the female but both reciprocal crosses always fail (Clausen, 1928). There is a similar situation with respect to an amphidiploid *paniculata-rustica* hybrid investigated by Lammerts (unpublished results). All these cases are in agreement with the general rule. Of the numerous crosses between species with the same chromosome number only three are reported to have given different results reciprocally.

The genus *Brassica* furnishes many critical cases. Sutton (1908) reported that when swede (*B. napus*) ♀ is

crossed with turnip (*B. rapa*) ♂ abundant plump seeds are produced, while the reciprocal yields only small shriveled seeds which germinate badly. Swede has eighteen chromosomes (haploid) and turnip ten (Karpechenko, 1922). Nelson (1927) obtained results similar to those of Sutton. Kajanus (1917) secured 437 good seeds from thirty-eight pollinated flowers in rape (18) ♀ x turnip (10) ♂, but only thirteen poor seeds from nineteen flowers in the reciprocal. Sinskaia (1927) reported results of numerous interspecific crosses in *Brassica* but only two of them in such a way as to enable one to distinguish between reciprocals. *Napus* (18) ♀ x *pakinensis* (10) ♂ gave more and better seeds than the reciprocal, and *juncea* (18) ♀ x *chinensis* (10) ♂ was difficult to make while the reciprocal was impossible. The chromosome numbers shown are those reported by Karpechenko (1922) and by Terasawa and Shimotomai (1928). The findings of the latter authors which are important in the present connection are given in Table II. In each case where the female has the larger chromosome number the

TABLE II

RESULTS OF SOME RECIPROCAL CROSSES IN *Brassica* (DATA FROM TERASAWA AND SHIMOTOMAI, 1928)

	Number of flowers pollinated	Number of seeds
B. cernua (18) ♀ × *B. chinensis* (10) ♂	30	30
reciprocal	30	3
B. cernua (18) ♀ × *B. pekinensis* (10) ♂	30	67
reciprocal	30	2
B. juncea (18) ♀ × *B. oleracea* (9) ♂	30	54
reciprocal	30	0
B. chinensis (10) ♀ × *B. oleracea* (9) ♂	30	3
reciprocal	30	0
B. pekinensis (10) ♀ × *B. oleracea* (9) ♂	50	3
reciprocal	50	1
B. chinensis (10) ♀ × *Raphanus* (9) ♂	30	12
reciprocal	30	0
B. pekinensis (10) ♀ × *Raphanus* (9) ♂	60	10
reciprocal	30	1

results are better than in the reciprocal. Crosses of *campestris* (10) with *cernua* and *juncea* gave about the same results in both directions. Morinaga (1928, 1929) stated that hybridization experiments with species of *Brassica* had been carried on extensively in his laboratory for several years and listed the ones which proved successful. In many cases, particularly where the parents had the same chromosome number, the reciprocals are mentioned as successful. But in the following cases, in addition to some dealt with by Terasawa and Shimotomai, the reciprocals are not mentioned:

cernua (18) ♀ x *rapa* (10) ♂
cernua (18) ♀ x *japonica* (10) ♂
juncea (18) ♀ x *pekinensis* (10) ♂
napella (19) ♀ x *japonica* (10) ♂
napella (19) ♀ x *juncea* (18) ♂

Fukushima (1929) tried repeatedly to cross *Raphanus* with various species of *Brassica* and obtained hybrids with *B. cernua* (18) and *B. juncea* (18) only when *Raphanus* (9) was male. On the other hand, with *B. oleracea* (9) hybrids were obtained only when *Raphanus* was female, a result also obtained by Karpechenko (1928). The latter author also reported that his *Raphanus-Brassica* with double chromosome number can be successfully used as female in crosses with *Brassica,* but not as male.

In general the numerous cases in *Brassica* in which the results of reciprocal interspecific crosses differ support our contention except *Raphanus* x *B. oleracea.* Since the chromosome numbers in this case are the same some other factor must be responsible.

When *Linum usitatissimum* is used as female parent in crosses with *L. perenne, austriacum, grandiflorum* and *flavum,* seeds of a poor quality are formed, but in the reciprocals no seeds at all appear (Tammes, 1928). In *usitatissimum* the haploid number is fifteen and in the others nine or ten. Eyre and Smith (1916) have re-

ported similar results in crossing *L. monogynum* with several other species, but so far as I can find the chromosome numbers of these species have not been reported. Laibach (1925) found that in crosses of *L. alpinum* ♀ with *L. perenne* ♂ and *L. austriacum* ♂, the seeds, though poor, are distinctly better than in the reciprocals. The chromosome number of *alpinum* is eighteen, according to Kikuchi (1926), and nine according to de Vilmorin and Simonet (1927). Laibach also found that in *perenne* ♀ x *austriacum* ♂ the seeds are better than in the reciprocal though in both cases they can be made to germinate by special methods. The other cases reported by Laibach either involve no difference in reciprocals or species of which the chromosome number is unknown.

Digitalis lutea can be crossed with *D. purpurea* much more easily when the former is female than when it is male (Wilson, 1906). The chromosome number of *lutea* is forty-eight and of *purpurea* twenty-four (Hasse-Bessel, 1916). From seventy flowers of *D. gloxinaeflora* pollinated by *D. lutea* Warren (1924) obtained more than 4,000 seeds, but from thirty flowers of the reciprocal only five seeds. The *gloxinaeflora* had twelve chromosomes and the *lutea* eight. Warren was aware of the difference in number between his *lutea* and Hasse-Bessel's and thought that his form, having come from Natal, was probably distinct from hers.

Jorgensen succeeded in crossing *Lamium dissectum* (18) with *L. amplexicaule* (9). The reciprocal cross failed though the experiment was performed on a large scale. Salaman (1928) made numerous attempts to cross *Solanum utile* (36) and *S. tuberosum* (24). He succeeded only when *S. utile* was female. Chittenden (1928) found that *Godetia lepida* (26) can be successfully crossed with *G. tenella* (16) only when *lepida* is female.

In a number of cases diploids have been crossed reciprocally with their tetraploid derivatives and tetraploid ♀ x diploid ♂ has given the better results. This

is true of *Campanula persicifolia* (Gairdner 1926), *Primula sinensis* (Keeble, 1912), and *Solanum nigrum* (Winkler, 1916). It is doubtful, however, to what extent such cases are applicable to the present problem because gamete formation is usually irregular in tetraploids and in such cases female gametes usually function better than male. (This consideration applies more forcibly to crosses involving triploids which are therefore not discussed.) Moreover, in interspecific crosses the difference between reciprocals is probably due not only to the fact that in the endosperm the excess chromosomes are present in the n or 2n condition but also to the fact that they are genetically distinct from those in the 3n condition. This is not true in crosses between diploids and their tetraploid derivatives. Bucholz and Blakeslee (1929) have shown that in crosses between 2n and 4n *Datura* a marked difference between reciprocals is due to abnormal growth and bursting of 4n pollen tubes in 2n stigmas.

An apparent exception to the general rule which holds in the cases already mentioned is found in *Fragaria* as reported by Mangelsdorf and East (1927). They succeeded in producing seeds in crosses between *F. vesca* (7) ♀ and *F. elatior* (21) ♂, *chiloensis* (28) ♂, *glauca* (28) ♂, and *virginiana* (28) ♂, between *F. americana* (7) ♀ and *glauca* (28) ♂ and between *bracteata* (7) ♀ and *virginiana* (28) ♂. The general statement is made that all reciprocals were failures, but no details as to numbers, etc., are given. Only a very small percentage of the seeds which they obtained would germinate and those which did germinate produced very weak seedlings, nearly all of which died at an early stage. Longley (1926) showed that such seedlings were maternal and probably the result of parthenogenetic development. The only cross reported by Mangelsdorf and East between species with different chromosome numbers, in which an abundance of good hybrids was obtained, was *virginiana* (28) ♀ x *elatior* (21) ♂. In this case the re-

ciprocal was unsuccessful and it therefore agrees with the general rule which obtains in the other genera.

Another apparent exception has been reported by Crane and Lawrence (1929) in *Prunus*. When sour and sweet cherries are crossed there is slightly better seed setting if the sweets are female, though they have the smaller chromosome number—sours thirty-two, sweets seventeen to nineteen. But the aneuploid condition of the sweets would probably cause a greater fertility of the female than of the male gametes, as has been shown to be true of many other aneuploid types.

A somewhat similar situation was found by Swarzenback (1922) in *Cardamine*. *C. bulbifera* (about 48) gave somewhat better results in crosses with *C. pinnata* (24) and *C. pentaphylla* (24) when it was male. But the chromosome behavior of *C. bulbifera* is irregular at the heterotypic division with many single chromosomes, and its fertility when pollinated by other *bulbifera* plants is low.

It is believed that the cases reviewed in this paper include most of those reported in which different degrees of success have followed reciprocal interspecific crossing, and in which at the same time the chromosome conditions of the parents are known. No case has been intentionally omitted. Many additional cases have been noted in which reciprocal crosses differ in success or difficulty but in regard to which cytological information is not available. Many reports also were noted of successful difficult crosses in which nothing was said about the reciprocals. In so far as their chromosome situations are known these were in line with the general rule.

The number of cases reviewed appears to warrant the conclusion that in cases in which reciprocal interspecific crosses differ in success or difficulty, the more successful is generally the one in which the species with the larger chromosome number is used as female. The difference appears to be due to the difference in the chromosome conditions of the endosperm. When the species with the

larger number is female the excess of its chromosomes over those of the other species will be doubled in the endosperm, whereas when it is male they will be single. The single condition of some chromosomes may of itself cause poor endosperm development, or more probably the association of the single condition of some with the triple condition of others is responsible. The endosperm is important even in those Angiosperms in which there is very little in the mature seed because it is used up during the development of the seed.

It is not contended, of course, that this cause of a difference between reciprocal crosses is the only one. There is at least one and probably several other causes. It has been shown that in some cases a difference in the length of the style is responsible (*Mirabilis* and *Polemonium*). It is possible that the pollen tubes of one species may grow abnormally in the styles of the other as do those of 4n *Datura* in styles of 2n. There may be other as yet undemonstrated causes such as a faulty interaction between the cytoplasm of one parent and the genes of the other. A number of cases have in fact been mentioned in which there is a considerable difference in the success of reciprocal crosses although the chromosome numbers of the parents are the same.

But the large number of cases in which the more successful cross is that in which the female parent has the larger chromosome number, and the demonstration in wheat of the relationship between chromosome conditions and the shriveling of the endosperm, indicate that this cause is at least an important one. If difficulty is experienced or anticipated in making a wide cross it is advisable to use the type with the larger chromosome number as the female.

SUMMARY

In crosses between species which differ in chromosome number the cytological situation in the endosperm depends on the direction of the cross. If the species with the larger number is used as the female the chromosomes

which it possesses and which the other lacks will be doubled in the endosperm, whereas in the reciprocal cross they will be single. In wheat the endosperm in which the excess chromosomes are doubled is normal, whereas that in which they are single is shriveled. Consequently when the species with the larger number is female the cross is more successful than when it is male. A review of the literature shows that as a rule the results are similar in other genera of plants: in cases in which reciprocal interspecific crosses differ in success the more successful is generally the one in which the species with the larger chromosome number is used as the female. There are also other causes of a difference in success, such as a difference in the length of the styles or possibly a faulty interaction of the cytoplasm of one parent and the genes of the other.

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EFFECT OF LECITHIN ON THE SEX RATIO IN THE ALBINO RAT

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TWENTY-ONE years ago Russo (1909) published the results of experiments designed to show the influence of lecithin upon sex determination in rabbits. He interpreted his data as demonstrating that the normal sex ratio could be altered by lecithin administration in favor of females. Similar results were said to follow whether lecithin was given by mouth, subcutaneously or intraperitoneally, and whether both parents were treated or only the female. Russo also claimed that the lecithin procedure vitiated the normal expression of the Mendelian mechanism of coat color inheritance (1909). Both conclusions have met either denial or skepticism.

However, if the explanation of sex determination in terms of differential metabolism (Geddes and Thomson, 1901) or metabolic rate (Riddle, 1916) is correct, then Russo's theoretic interpretation of his experimental materials with respect to altered sex ratios seems worthy of serious consideration. The interpretation is in accord with Geddes and Thomson's conclusion that "the female is the outcome and expression of relatively preponderant anabolism and the male of relatively preponderant katabolism." Starting with the facts: (1) That in those cases where a relationship obtains between size of egg and sex bias, it is always the larger eggs that develop into females; (2) that size of egg is correlated with the amount of yolk; (3) that yolk is largely lecithin—Russo argues that the introduction of lecithin into the body should increase the relative number of larger (more heavily yolk-laden) eggs. Microscopical examination of ovarian eggs in his experimental animals seemed to disclose a numerical augmentation of the larger ones.

These eggs showed an increased mitochondrial content. Mitochondria are closely associated with yolk production (Cowdry, 1918). Heape (1908) suggests that Russo's so-called male ova are in reality degenerate.

The essential data upon which Russo based his conclusion are reproduced in Chart I. He states in his memoir

CHART I.—RUSSO'S DATA

Control rabbits			Lecithin-treated rabbits		
Mothers	♂	♀	Mothers	♂	♀
1	4	3	1	4	4
2	3	2	2	1	4
3	4	1	3	2	5
4	5	4	4	3	5
5	4	3	5	3	4
6	5	3	6	2	4
7	3	5	7	3	4
8	3	2	8	2	3
9	3	3	9	3	4
10	2	3	10	3	5
Totals	36	29		26	40
Sex ratio	124.1	100.0		65.0	100.0
	3	2½		3	5

of 1909 that these results are similar to those in an earlier series of experiments, including more than one hundred lecithin-treated females. He points out that such results obtain only with first litters, or in cases where the offspring were weaned at twenty days and a rest period of at least two months allowed between successive litters. Since in mammals the fundamental sex-determining mechanism is presumably chromosomal, depending upon the occurrence of two kinds of sperm, male and female determining, it must be concluded that the alleged lecithin effect is one of overriding of the chromosomal influence.

Russo's data show a sex proportion in favor of males (36 ♂ : 29 ♀) in the total litters of ten untreated (normal) rabbits. The combined litters of the same number of lecithin-treated rabbits show a reversed proportion in

favor of females, namely 26 ♂ to 40 ♀. Both series of litters covered approximately the same season (February to April), thus eliminating a possible differential factor of seasonal variation. But these series seem much too limited to warrant a definite conclusion.

In his earlier paper Russo (1907) compared 100 control litters with 100 litters from lecithin-treated does. The controls totaled 400 ♂ and 287 ♀. The experimental litters gave a total sex ratio of 217 ♂ to 431 ♀. This result shows a proportional increase of females of approximately 25 per cent. But the conclusion becomes highly dubious since Russo included in his totals of lecithin-affected litters only those in which the number of females preponderated. A repetition of Russo's experiment by Basile gave a negative result. Basile (1908) secured a ratio of 66 ♂ to 51 ♀ from 117 individuals in 17 litters from 6 injected does. In his control material of 440 offspring in 60 litters the ratio in favor of males was actually lower than in the experimental material, namely 225 ♂ : 215 ♀. Punnett (1909) also failed to confirm Russo's results. He used exclusively the feeding method of administering the lecithin. He secured 47 young from 10 does, in the ratio of 24 ♂ : 23 ♀. A control series of 18 litters gave a ratio of 54 ♂ : 49 ♀. These series of Basile and Punnett are open to the same objection as that of Russo; they are too limited in scope.

We have undertaken a repetition of Russo's lecithin experiments with respect to sex determination. We selected the albino rat, secured from the Wistar Institute, for our experimental animal. In order to determine first the normal sex ratio in our material, and under the condition of housing and feeding in our colony, we collected seventy-five litters from 49 individuals through a period of one year. The data are tabulated in Chart II. The letters A, B, C and D indicate successive litters from the same female; thus, A–86 means that 86 different first litters had been examined in the several series of experiments at the time this table was compiled. The totals of

CHART II.—Sex Ratio of Normal Litters

Mother's No.	Litter No.	♂	♀		Mother's No.	Litter No.	♂	♀	
2	A– 1	2	8		37	A–41	8	7	
1	A– 2	9	4		33	A–44	4	6	
3	A– 3	9	6		34	A–45	7	4	
2	B– 5	3	3		32	A–46	5	5	
6	A– 6	4	4		44	A–47	5	5	
4	A– 7	4	4	60 ♂ : 46 ♀	36	A–48	2	8	
6	B– 8	6	3		19	B–49	5	4	
2	C– 9	3	7		59	A–56	6	7	
4	B–10	8	7		50	A–67	1	0	
8	B–26	6	6		37	B–53	7	4	
17	B–40	8	2		40	A–54	4	5	
9	C–50	7	5		42	A–55	2	5	
7	C–51	3	8		51	A–58	4	3	
54	A–57	5	7		49	A–59	7	5	
52	A–61	9	3		48	A–60	6	1	
1	B– 4	2	2		55	A–63	5	5	
9	A–11	8	6		46	A–64	6	5	
7	A–12	8	6		36	B–66	4	10	
15	A–13	5	7		56	A–68	5	4	
8	A–14	8	6		45	A–69	6	7	
16	A–15	4	5		44	A–70	5	2	
10	A–16	6	8		7	D–71	2	2	
3	B–18	3	2		53	A–72	6	6	38 ♂ : 47 ♀
15	B–19	9	4		65	A–73	1	9	
7	B–20	5	4		47	A–74	7	5	
9	B–21	1	5		20	C–75	3	5	
17	A–22	5	6		57	A–76	3	6	
19	A–23	4	5		64	A–77	0	1	
18	A–24	10	2		59	B–78	6	6	
20	A–28	6	6		41	B–79	6	7	
22	A–32	2	2		19	C–80	8	5	
21	A–33	1	2		63	A–81	6	5	
15	C–34	6	5		66	A–82	4	6	
10	B–35	4	3		58	A–83	8	2	
38	A–36	5	5		67	A–84	3	6	
41	A–37	5	4		8	D–85	5	3	
20	B–38	7	6		60	A–86	3	1	
8	C–39	1	6				375	361	

Normal sex ratio, 103.9 ♂ per 100.0 ♀

375 ♂ to 361 ♀ gave a ratio close to unity, actually slightly in favor of males (103.9 ♂ : 100.0 ♀). This agrees fairly closely with King's (1927) figure for all her series of rats (16,487 litters, 113,709 individuals, Table 5) covering one complete year, namely 100.45 ♂ to 100.0 ♀. Taking individual months her figures vary from 103.7 ♂ : 100.0 ♀ for the month of April, to 97.79 ♂ : 100.0 ♀ for the month of

November. On the other hand, Russo's series of ten normal litters gives a ratio more in favor of males, namely 36 ♂ to 29 ♀ or 124.1 ♂ : 100.0 ♀. The ratio more nearly approximating this in King's series (hybrid and piebald rats, Table 4) is the one for the January total of 1,107, namely 114.57 ♂ : 100.0 ♀. Our control litters (Chart IV) give a very similar ratio, 118.6 ♂ : 100.0 ♀.

Returning to our Table II, a striking feature appears in the enormous variation of the sex ratios. The suspicion that certain females may be hereditarily biased as male or female lines, and against which possibility we tried to guard in the experiment tabulated in Chart IV, has apparently no basis. For example, litters A–14, B–26, C–39 and D–85 (Chart II) are from the same female (No. 2) at successive birth periods. The sex ratios of these litters are respectively 8 ♂ : 6 ♀, 6 : 6, 1 : 6 and 5 : 3.

Our first series of data is tabulated in Chart III. The litters represented are from seven different lecithin-treated females. They are first, second and third litters. The season was December to January. Again the varia-

CHART III.—SEX RATIO IN LITTERS OF LECITHIN-INJECTED RATS

Mother's No.	Litter No.	♂	♀
12	A– 25	1	9
23	A– 29	5	9
24	A– 30	5	7
30	C– 52	2	8
1	C– 17	2	5
25	A– 27	2	2
30	A– 31	4	5
23	B– 42	7	6
12	B– 43	3	3
23	C– 62	7	7
12	C– 65	4	7
62	A– 99	3	2
43	A–105	4	3
		49	73

A. Litters with no control.
Sex ratio, 67.1 ♂ per 100.0 ♀.

tion in the sex ratio of individual litters is striking. The ratio of the totals is equally arresting. The proportion of 49 ♂ to 73 ♀, giving a ratio of 67.1 ♂ : 100.0 ♀, was so different from the normal (103.9 ♂ : 100.0 ♀) and so close to that of Russo's series (65.0 ♂ : 100.0 ♀) that it seemed to confirm fully Russo's claim of the sex-determining influence of lecithin. This series, though slightly more extensive than those of Russo and of Punnett, is again too small to meet properly the objection of fortuity.

To test the matter further a new series with controls (Chart IV) was begun in January and continued to November. The unfortunate appearance in November of

CHART IV.—SEX RATIO IN LITTERS OF LECITHIN-INJECTED RATS

Control			After Lecithin			
Litter No.	♂	♀	Mother's No.	Litter No.	♂	♀
A–74	7	5	47	B– 87	7	2
A–69	6	7	45	B– 88	6	6
A–37	5	4	41	C– 89	0	6
D–85	5	3	8	E– 90	7	5
A–54	4	5	40	B– 91	6	3
A–86	3	1	60	B– 92	5	4
A–64	6	5	46	B– 93	7	6
A–59	7	5	49	B– 94	4	8
C–34	6	5	15	D– 95	1	2
A–60	6	1	48	B– 96	7	5
A–46	5	5	32	B– 97	3	10
A–44	4	6	33	B– 98	0	3
A–77	0	1	64	B–100	4	1
A–76	3	6	57	B–101	2	1
A–58	4	3	51	B–102	2	2
A–81	6	5	63	B–103	2	7
A–67	1	0	50	B–104	5	4
A–55	5	5	55	B–106	3	6
A–83	8	2	58	B–107	2	3
A–72	6	6	53	B–108	0	2
B–78	6	6	59	C–109	3	4
A–86	3	1	60	C–110	4	5
A–68	5	4	56	B–111	2	2
A–64	6	5	46	C–112	2	8
A–44	4	6	33	C–113	4	2
	121	102			88	107

B. Litters with one control litter.

Sex ratio, 118.6 ♂ per 100.0 ♀ — 3 : 2½

Sex ratio, 82.3 ♂ per 100.0 ♀ — 4 : 5

a bacterial infection in our colony introduced a possibly vitiating factor, and it seemed best to terminate the experiment, short of the number of litters we had hoped to secure. Twenty-five litters were available at this time. The litters to the left are first litters, those to the right are the second litters of the same females at the same levels. Five lecithin-treated males were employed. The results are again striking, but of slightly less degree. The total sex ratio of the normal litters (118.6 ♂ : 100.0 ♀) approximates that of Russo's series (124.1 ♂ : 100.0 ♀); similarly the total ratio of the litters from the same lecithin-treated mothers, 82.2 ♂ : 100.0 ♀, as compared with that of Russo's series, namely, 65.0 ♂ : 100.0 ♀.

In these experiments we followed Russo's technique as closely as possible. He rightly claims, in arguing against the non-confirmatory evidence of Basile and Punnett, that a legitimate test of his results must employ his exact technique. In the earlier experiments (Chart III) we used vaseline oil as recommended. However, we found that olive oil was absorbed more readily, and in the later experiments (Chart IV) we used this, supersaturated with lecithin, approximately 40 grams of lecithin to 100 cc of the oil. The lecithin was obtained from the Eastman Kodak Company. Injections of 2 cc were made at three-day intervals, a total of five being given, alternating subcutaneous injections in the flank with intraperitoneal injections. After the last injection a rest period of ten days was allowed before mating. The females gained in weight during the period of treatment. The amount varied among the different individuals, but averaged about 25 per cent. An interval of approximately two and a half months intervened between the two litters (Chart IV). The greatest care was exercised in guarding against the eating of the newly born before the sex could be determined. We feel confident that every individual born is properly accounted for in our tables. A few doubtful litters were discarded.

While our results parallel those of Russo, the significance of both with reference to a specific sex-determining influence of lecithin seems doubtful by reason of the fact that both in the control and experimental series the individual litters varied greatly, with preponderance respectively in favor of both males and females. Moreover, while most groups of ten consecutive litters in the first control series of seventy-five litters (Chart II) show a preponderance of males, a few groups may be selected in which the preponderance favors females.

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NATICA AS A RADICLE

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NATICA or the naticoid type holds a unique place in the ontogeny and phylogeny of the coiled Gastropoda. Its position in the history of the race has been admirably pointed out by Grabau[1] in his "Studies of Gastropoda," and in his treatise on the "Phylogeny of Fusus and Its Allies."[2] There would be little cause at this time to take up the discussion again, if it were not for the fact that certain new data pertaining to the development of some Paleozoic, Mesozoic, Cenozoic and Recent forms have been observed. The basis for classification as presented by Dall,[3] Ulrich,[4] Grabau[5] and others will probably always be argued pro and con, depending upon the point of view of the zoological systematist at the time he makes a study of the living forms. His material for study consists or should consist of the entire living organism; consequently he is able to trace the ontogeny of an individual in detail. But, to the paleontologist, who is dependent upon the shell of the fossil gastropod for his study, the emphasis is placed on the shell development as a means of formulating a natural classification.

The fundamental law governing the development of races was briefly stated by Alpheus Hyatt, "Ontogeny recapitulates phylogeny." This, to Hyatt, was not a new concept, for Louis Agassiz, in 1847, stated, "The Lord brings back in the young those types that have gone be-

[1] A. W. Grabau, "Studies of Gastropoda, I, II and III," THE AMERICAN NATURALIST, 36: pp. 917–945, 1902; 37: 515–539, 1907; 41: 607–653, 1907.

[2] Smithsonian Miscellaneous Collections, vol. 44, 1904, No. 1417, 157 pp.

[3] W. H. Dall, "Contribution to the Tertiary Fauna of Florida," *Trans.*, Wagner Free Inst. Sci., 3: 67; vols. 3 and 5.

[4] E. O. Ulrich and W. Scofield, "The Lower Silurian Gastropoda of Minnesota," "The Geology of Minnesota," vol. 3, part 2, 1892–96, pp. 813–1081, plates 61–81.

[5] A. W. Grabau, *ibid.*, vols. 36, 37 and 41.

fore." This law of recapitulation has been tested repeatedly, and has been found correct in every instance where the complete data for the study have been available; therefore it can be accepted without argument or reservation.

An attempt at a genetic classification of the Gastropoda is based upon the study of the protoconch and early stages of growth of the shell. It takes into consideration the adult and senile characters to show specific or even closer relationship. Grabau's classification[6] might lead to confusion unless one recalls that the initial whorl of each type is naticoid in form, for the early whorls of the protoconch of most gastropods are smooth, rounded and obliquely set. *Luniatia heros* exemplifies the characteristic of the naticoid shell as well as any species, for in it the initial whorl is minute and the succeeding ones enlarge gradually and regularly.

Each type may be used for the study of the different groups of gastropods, and they may aid decidedly in determining the classification of this class of animals from a genetic standpoint. This basis of classifying fossil forms is satisfactory providing sufficient protoconchs and early stages can be studied. In his analysis of *Fusus,* for instance, Grabau[7] indicates that the earliest whorls and particularly those of the protoconch are characteristic of the genus, and states, "No species which does not show a protoconch similar to that of *Fusus colus,*

[6] AMERICAN NATURALIST, 36: 919–920, 1902.

Types of protoconch:

(1) Bulbous. The initial whorl is large and swollen, generally elevated and oblique. (*Fusus, Hemifusus, Fulgar,* etc.)

(2) Trochoid. The initial whorl compressed to form a cone, with sloping sides flat. (*Clavilithes,* etc.)

(3) Melo. The continuation of the naticoid type. (*Melo,* etc.)

(4) Planorboid. Whorls depressed so as to nearly lie in a plane.

(5) Pupiform. The naticoid initial whorl is succeeded by a number of whorls which increase slightly or not at all in size, thus giving a long and slender type.

[7] Smithsonian Miscellaneous Collections, vol. 44, No. 1417, 1904, especially pp. 1–11.

the type of the genus, can be relegated to *Fusus.*" Thus the protoconch of *Fusus* is distinctive and has been observed in twenty-one species. The protoconch of *Fusus* consists usually of one and a half volutions. The first whorl is always smooth, obliquely set and prominent, thus naticoid in form. The later characters are introduced in the ananepionic stage, consequently the genus is an extremely accelerated type.

The primitive ornamentation of gastropod shells consists of vertical ridges or ribs and revolving spirals. Usually the vertical ribs are first introduced, probably as a result of thickening due to the retardation of growth in the early stages. Other ornamentation follows in progressively more complex order. It is a well-known biogenetic law that all phyletic characters appear in a definite order in the ontogeny of an individual, which merely represents each progressive stage of growth of the group. Thus the shell characters appear in definite order. For example, *Cyclonema humerosum* Ulrich,[8] a specimen obtained from the Maysville formation of Cincinnati, Ohio, shows that the fine vertical costae are introduced in the nepionic stage and the revolving spirals in the ananeanic stage. The protoconch is a simple naticoid form.

The phyletic acceleration, or the condensation and elimination of certain stages of growth, can be observed in the shell of the gastropods, similar to that which is observed in other classes of invertebrates. The law naturally follows that the farther a stock is removed from the parent radicle the more highly accelerated the parent characters are in the ontogeny of the individual comprising the stock. Thus if any primitive character appears in the protoconchs of the highly divergent stocks which can be attributed to the simple early form it would be indicative that such a form served as a parent from which the divergent stocks branched, and thus can be considered the radicle for the entire group. *Natica* is such a form.

[8] Many of the specimens referred to in the following pages are in the author's personal collection.

It has not been proven that all coiled gastropods have as their ancestor a naticoid type; however, the study of the different genera leads one to that conclusion. This deduction is strengthened when many coiled gastropods of Paleozoic age have been studied and found to be naticoid in shape either during their entire development or during the early part of their development; moreover, not a single protoconch has been observed by the author which is not a naticoid type.[9]

The basis for determining the radicle relationship of *Natica* is naturally the study of the shell. The shell description of *Natica* is, according to Tryon:[10]

> Shell globular or oval, spire usually short, aperture semicircular, without canal or anterior notch, the outer lip sharp, the columellar lip callous, more or less reflected over the umbilicus. . . . Operculum paucispiral, corneous, or with an exterior calcareous layer. Dentation, 3–1–3.

Dall's[11] description is very similar:

> Shell with short spire and large body whorl, globose, semiglobose, ovate or pyramidal, smooth and lustrous, umbilicate or not. The umbilicus, when present, often partially or entirely filled with a callus.

These descriptions fulfil all the requirements of the description of the protoconchs of the coiled gastropods, except that in the protoconchs a callus is not formed closing or partly closing the umbilicus. This could not occur, since the conch develops directly from the protoconch without retardation, except in the highly accelerated forms.[12]

The fossil evidence of the primitive stock occurs in the Lower Cambrian in *Straparollina remota* Billings. This is a naticoid form. It is a depressed conical to discoidal shell, spirally coiled and more or less deeply and widely

[9] The author has examined hundreds of specimens of gastropods of Paleozoic, Mesozoic, Cenozoic and Recent ages.

[10] Geo. W. Tryon, "Conchology, Systematic and Structural," p. 126.

[11] W. H. Dall, "Gastropoda." Zittel, "Text-Book of Paleontology," Estman's Edition, 1913, p. 542.

[12] The protoconch of the Gastropoda has been figured so many times that no figures accompany this paper.

umbilicate. *Straparollina* ranges to the Silurian and could have given rise to several stocks. The protoconch of *Maclurea,* Ordovician and Silurian, has been observed and found to be naticoid in form. Thus *Maclurea* is closely allied to the primitive ancestor. The protoconch of *Cyclonema* is naticoid, and the spiral ornamentation is introduced early in the neanic stage of growth. Probably one of the earliest ribbed gastropods is *Holopea pyrene* Billings, which is found in the middle and upper Trenton of the United States and Canada. According to Ulrich's[13] figure of this species, the protoconch and first whorl are naticoid, and without ornamentation. Ulrich's figure of *Fusispira nobilis* U. and S.[14] Trenton group indicates that this type of shell possessed a naticoid protoconch, although the spirals are not introduced until the seventh volution. Many of Ulrich's figures illustrating many genera indicate that the protoconchs are naticoid. These figures include some of the more divergent Ordovician stocks. The naticoid protoconch has been observed in *Diaphorostoma niagarensis,* Silurian; *D. lineata,* Onondaga; *Euomphalus utahensis,* Madison; the high spired *Aclisiina* sp. indt., Park City; *Worthenia tabulata,* Coal Measures (Cisco), and *Trepospira sphaerulata,* Coal Measures. Many more Paleozoic genera undoubtedly possess a naticoid protoconch. Grabau[15] states that *Natica mexicosta* Phillips, Devonian, is truly naticoid. The earliest stages are smooth. The later whorls possess sharp, narrow and uniform ribs. He states further that "The whole aspect of the last whorl of this shell is strikingly like the final whorls of the protoconch of highly specialized Tertiary and recent gastropods." *Natica subcostata* Schl., Stringocephalen Kalk, possesses costae or ribs which have become compound. Grabau thinks that *Natica costata* of the Lower Triassic of Ft. Cassian

[13] E. O. Ulrich, "The Lower Silurian Gastropods of Minnesota," "The Geology of Minnesota," vol. 3, part 2, 1897, pl. 79, figs. 13–18.

[14] *Ibid.,* pl. 80, fig. 3.

[15] AMERICAN NATURALIST, 36: 926, 1902.

carries the simple type of costae into the Mesozoic era. The only gastropod thus far found by the author in the Pinecrest formation, Lower Triassic, of the Fort Douglas Area, Utah, is a very small naticoid form. This gastropod is about the size of a blunt pin point. It consists of one and a half to two and a half whorls, possesses an umbilicus and has all the characteristics of the protoconch of the more highly developed Paleozoic, Mesozoic, Cenozoic and Recent gastropods. One specimen has the primitive characters or ribs of *Fusus* on the third or last whorl; the shape also of that volution is somewhat fusiform. This discovery indicates that the radicle was carried over into the Mesozoic in the simple naticoid form, and there rapidly deployed, one branch forming the fusiform stock.

Fossil evidence of later stocks occurs throughout the Mesozoic, Cenozoic and Recent times. The *Natica* living to-day is apparently as rigorous as at any time during its life history. There are many examples of the naticoid protoconch among the more divergent stocks of these later periods. The type occurs in *Gyrodes depressa,* Colorado; *Turritella coalvillensis,* Frontier; *Pyrgulifera humerosa,* Upper Cretaceous; *Lunatia occidentalis,* Fox Hills; *Anchura americana,* Fox Hills; *Oliva literata,* Pliocene; *Solenosteria mengeana,* Pliocene; *Strombus pugilis,* Pliocene, and the more divergent recent and living genera, *Marginella, Cypraea, Harpa, Strombus, Murex, Pupura,* etc.

From the preponderance of evidence presented in the study of the coiled gastropods, one is led to believe that *Natica* or the naticoid type has served as a radicle stock, and that most if not all the genera of coiled gastropods have branched off from this parent stock. Once separated, these branching stocks developed more and more complex characters and established themselves in parallel lines of evolution.

THE FIRST MORNING SONG OF SOME BIRDS OF WASHINGTON, D. C.; ITS RELATION TO LIGHT[1]

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MY interest in the singing behavior of birds began in earliest childhood. This interest has become intensified as a result of the work of W. W. Garner and myself dealing with the effects of length of day upon growth and reproduction in plants. The present paper is intended to be more or less supplementary to an earlier historical contribution (1928) dealing with opinions and theories of bird migration from the point of view of light and changes in the seasonal length of day. Since it is obvious that the various rhythms of day and night govern many of the common rhythms of plant and animal behavior in one way or another, it is evident that every phase of behavior should be expected to be more or less closely synchronized with these influences. The singing of the birds is not least among these.

The first morning song of birds has been given more or less attention by a number of field naturalists. To the most casual observer, it is obvious that many birds awaken very early since their singing begins long before actual sunrise. So well is this appreciated in the country that many people are greatly disturbed in their morning sleep by the early dawn medley from dozens of vociferous birds. It would appear that the first morning song of the various birds is a function of some early phase of daybreak. It is easily seen that as the warm season advances from the spring equinox toward the summer solstice with the sunrise becoming progressively earlier each day, the earliest singing of the birds is advanced to keep pace with the phenomenon in a regular and proportionate way.

[1] This article was submitted in September, 1929.

Charles A. Witchell (1896, p. 2) in England was impressed with this relation and was perhaps the first to make the significant statement that on every successive morning near the end of May a thrush began its song about a minute and a half earlier each day, "so that we could predict almost to a minute the time when his first notes would be heard."

In America, Horace W. Wright has given considerable attention to the dawn singing of the birds. His first paper appeared in 1912, giving observations as recorded at Jefferson Highlands in the White Mountains of New Hampshire from May 27 to July 9, over a period of years from 1902 to 1911. Wright made some interesting observations and established with more or less finality for his locality the regular order of singing of a number of birds. His records, only fifteen in number, were too few and too scattered, through the season and through the years, however, to give any detailed picture of the more evident relationships of the first song with particular light conditions attending the coming of the dawn.

In 1913 Wright again published further observations of the first morning singing of birds in the regions of Jefferson Highlands, New Hampshire, for the period between June 20 and July 15 inclusive. In his first paper (1912) he was of the opinion that cloudiness and bright moonlight at dawn had no effect upon the time of the first singing. In his second paper he was inclined to modify this, and found that on one brilliant moonlight morning, June 19, the birds sang unusually early.

In 1913 Francis H. Allen published a paper on the morning awakening of the birds at Boston, Massachusetts. He took exception to some of the data as presented by Wright in his second paper (1913), where he gives the dawn singing of the chipping-sparrow and song-sparrow as earlier than that of the robin. He also considered the kingbird a close second to the robin in the order of the first morning singing, whereas Wright placed it long after the robin in its schedule of singing.

In 1919 H. E. Tuttle published observations of the first drumming sounds made by the ruffed grouse at Simsbury, Connecticut, in May. It is indicated that the drumming bird was moving about as early as 3.30 A. M. in some instances, since it came to its accustomed drumming log at that time.

In 1928 S. F. Blake published a brief note giving the time of retiring to roost for the night of the slender-billed nuthatch, *Sitta carolinensis aculeata,* at Palo Alto, California. Nine observations were made from June 29 to August 26, these indicating a nice correlation between the time of sunset and the time of retiring of the little bird some minutes earlier.

In 1929 Walter P. Taylor published brief notes giving the order of awakening of a number of birds near Flagstaff, Arizona, as observed on July 6.

G. M. Allen in 1925 in his excellent book "Birds and their Attributes" supposes light intensity to be the factor awakening the birds at dawn, and says (p. 220): "I have supposed that it was a factor of this sort that caused birds to awake in the morning, as by an alarm clock." He noted that the house-sparrows began their chirping at approximately fifteen minutes before the sun rose, awakening correspondingly earlier as the sun rose earlier in later summer. He mentions the behavior of the whippoorwills beginning their nocturnal serenades earlier on cloudy nights. He states that the crowing of the chanticleer "is of such regularity in the morning that people who live in or near the tropics, where sunrise does not greatly vary in time, make the cock-crowing equivalent to a rising bell" (p. 220).

Aretas A. Saunders (1929) discusses the morning awakening song and refers to the distinctiveness of the first singing of a number of birds including the robin, chipping-sparrow, vesper-sparrow, kingbird, crested flycatcher, phoebe, wood pewee.

This brief résumé appears to cover this phase of behavior of our American birds as considered by American field naturalists.

My interest in the matter from the point of view of a more critical understanding of the correlations began several years ago, and during the season of 1929 I carried out detailed and systematic observations for a number of birds around my home at Lyon Park, Virginia. Observations of the song-sparrow's first singing were begun in early January, and the others followed in their turn as they appeared in their migrations or began their springtime singing. In a study of this sort one must be an early riser, especially toward the summer solstice. At this period the birds, notably the song-sparrow, push their first dawn singing well down toward the beginning of astronomical twilight,[2] when the first phases of the coming day are reflected in the eastern and western skies. The sun itself advances its time of rising a few minutes each day from mid January to early June, until its earliest rising at the summer solstice is 4.41 A. M. eastern standard time. To obtain my data, I made it a point to arise from three quarters of an hour to one hour and a half before actual sunrise each day from January 15 to September 1, regulating this to correspond with the seasonal activities of the birds. During the period near and around the summer solstice, this required my own awakening as early as 3 A. M. for five to six weeks.

In general it may be said that the winter singing of such birds as the song-sparrow and the redbird is relatively near the sunrise, but as the vernal equinox approached a noticeable diverging of the dawn-song curve away from the actual sunrise curve became evident, and this continued until the maximum divergence was reached at the period of the summer solstice (Fig. 1). The song-

[2] Astronomical twilight is defined as beginning in the morning and ending at night when the center of the sun's disk has reached a point 18° below the true horizon. Civil twilight begins and ends when the center of the sun's disk is 6° below the true horizon. On brilliant nights and mornings when the sun is passing to and from these points respectively, certain well-marked phenomena become visible in the skies. These various phases have been very carefully studied by Bezold and others. See Kimball (1916); Bezold, Abbe's translation, etc.

sparrow, the redbird and the robin, more especially, gave evidence of an awareness of the dawn light, as it seems, far below the intensity values prevailing at the termina-

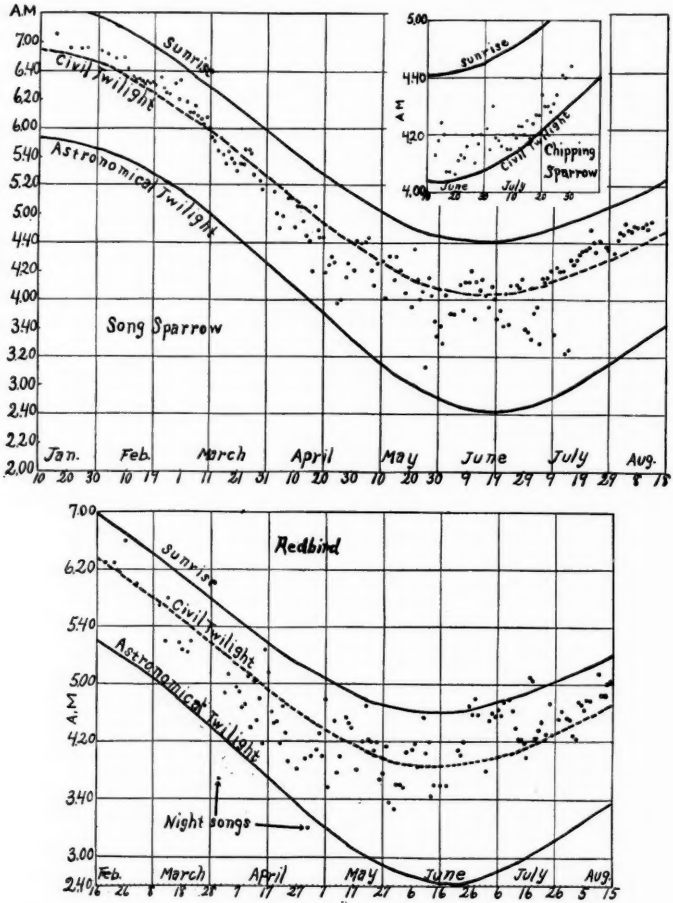

FIG. 1

First morning songs of the Chipping-sparrow, Song-sparrow and Redbird or Cardinal.

In the case of the Redbird, circles in August represent mere calls at the end of the song period. In all figures, all data, time of singing, sunrise, civil and astronomical twilight are given in eastern standard time.

tion of civil twilight. In fact, the earliest singing was associated with the very low values well on toward the beginning of astronomical twilight (Fig. 1).

In a study of the first dawn singing of the birds, one is confronted with various technicalities of definition and delimitation. Just as night merges by almost insensible gradations into day through a long series of twilight phenomena, so does the behavior of the birds now and then trend well into the night time. Often times a little bird sings at midnight or at any other hour of the true night. A number of our birds are rather given to this wakeful, or is it a veritable dream mood of nocturnal song? Among these are the chat, the ovenbird, the field-sparrow and the wood-pewee. I have heard the redbird sing buoyantly at midnight once. I have never yet heard the robin or the wood-thrush sing at these unseasonable hours. These are characteristics which appear to be more or less deep-seated within the species behavior. Of course we have our true night-singing birds like the whip-poorwill and our voluble mocking-bird given to tuneful singing all night long around the summer solstice period on fine moonlight nights.

There has been some doubt expressed as to what we shall consider a dawn song, to distinguish it from the true night song. The night song is born of some aberrant mood not definitely related to external or environmental conditions, it seems to me, and unquestionably it should not be included in one's data of the first dawn song. However, the night song is not a common and regular behavior. Furthermore, one may, if he chooses, find a convenient demarcation in the termination of the astronomical twilight, since this marks the first or last discernible feature of the coming or departing day. Any song falling sporadically much beyond the limits of the astronomical twilight of dawn may be considered a true night song. Let me add that any song falling within the limits of the astronomical twilight, as recognized by astronomers, can not be discarded as accidental or without purport in our data.

This is evident since already the first phases of the new day have begun for human vision. One must be chary of denying to creatures as highly sensitive as the birds in their nervous organization sensitivities to these phenomena that have begun to initiate the new day to our own visual sense. Whatever the latitude may be, as soon as the initiation of astronomical twilight appears phenomena are actually at hand to which the birds may perchance respond in one way or another. At those higher latitudes 50° and beyond, where the astronomical twilight of the evening is continuous with the twilight of the morning, the true night song can not be considered to enter, since in these high latitudes the last phenomena of the passing day are still at hand when the returning day begins. At 50° this persistence of astronomical twilight is an actuality for all of June and the period of July from July 1 to July 11, according to Herbert H. Kimball (1916). The total duration of astronomical twilight for the night and morning leaves a very small period of actual or true night in the higher latitudes at the period around the summer solstice. This can be seen in Table I.

Beyond the latitude 50° the astronomical twilight becomes continuous for increasingly longer periods through the midsummer season. At 52° it is continuous from May 22 to July 24; at 54° from May 13 to August 2; at 56° from May 6 to August 9; at 58° from April 29 to August 16, and at 60° twilight lasts from April 23 to August 22. It is to be expected that some of the birds will be affected by the higher light intensities of certain phases of this twilight phenomenon. As a matter of fact observers have reported the singing of the birds throughout the entire night in these latitudes. These instances of song expression can not be considered the true night song, however, since some phase of the twilight glow ever remains visible in the skies.

Edward Arnold (1912), making observations in Newfoundland near Port au Basques in early June, reports

TABLE I

SUNRISE, SUNSET, BEGINNING AND ENDING OF ASTRONOMICAL TWILIGHT AND THE DURATION OF THE TRUE NIGHT BETWEEN THESE TWO POINTS OF THE SUMMER SOLSTICE, JUNE 21, FOR THE HIGHER LATITUDES

Lat.	Time of sunset*	Time of sunrise*	Time elapsing between sunset and sunrise	Ending of astronomical twilight in evening*	Beginning of astronomical twilight at dawn*	True night or time between ending of astronomical twilight of evening and its beginnings at dawn
	hrs. min.	hrs. min.	hrs. min.	hrs. min.	hrs. min.	hrs. min.
50	8 — 13	3 — 50	7 — 37	....	....	.....
48	8 — 03	4 — 0	7 — 57	11 — 12	0 — 19	1 — 7
46	7 — 54	4 — 8	8 — 14	10 — 38	1 — 16	2 — 38
44	7 — 46	4 — 17	8 — 31	10 — 11	1 — 55	3 — 45
42	7 — 38	4 — 24	8 — 46	9 — 51	2 — 11	4 — 20
40	7 — 32	4 — 31	8 — 59	9 — 35	2 — 35	5 — 0
38	7 — 29	4 — 34	9 — 5	9 — 25	2 — 44	5 — 29

* Local civil time meridian of Greenwich: To obtain standard time for any point on a parallel of latitude, increase the time by the number of minutes the station is west of the standard meridian. For the latitude of 50° there is no true night since the twilight is continuous from sunset till sunrise for the period June 2 to July 12. Near 60° civil twilight becomes visible all night, and at 66° 33′ the sun itself remains visible with no disappearance below the horizon for one day. Its period of visibility increases progressively from this latitude to the pole (90°) where it does not set for 186 days 10 hours. (Annuaire de L'Observatoire Royal Belgique, 1893, p. 114.)

hearing the night calls and songs of birds, more especially Wilson's snipe, at all hours after sunset. At this latitude, about 48°, however, there are only about one and one half hours of true night, and many of the notes were probably within the long twilight periods prevailing there.

Thayer (1903) reports hearing in southern New Hampshire the *cow, cow* notes of the black-billed cuckoo all night around mid July. Here near the latitude of 43°, the true night between the beginnings and endings of twilight embraces a period of only about four and one half hours. It is probable that many of these notes came within the twilight periods.

Saunders (1929) reports hearing the ovenbird in Connecticut singing around 2 A. M. In this region a song

heard later than 2.30 A. M. is likely to be a twilight song more properly speaking.

It is possible that some of the so-called night singing of Nuttall's sparrow from April to mid June in the Washington and Oregon region as reported by Stover (1913) is associated with the long twilight periods prevailing between the latitudes 44° and 48° at this season.

The midwinter singing of the winter wren at Haddonfield, New Jersey, as reported by Rhoads (1895) is unquestionably a true night song, since it was heard long after the end of the twilight for that season.

In the Washington region, the astronomical twilight of sunset at the summer solstice, June 21, does not terminate until 9.25 P. M. and it begins at 2.44 A. M. Between these points there is a period of five hours and twenty-five minutes when true night may be said to obtain.

In my own observations I have regarded all singing within this period of true night as sporadic and pertaining to other conditions than the influences of the coming day. As a matter of fact, none of the birds which I had under observation were given to erratic night singing except in very rare instances. Not long after the beginning of the astronomical twilight of dawn, however, a number of birds, including more especially the song-sparrow and the redbird, began persistent singing through late May and June, showing that in some manner they were aware of the approach of the new day long before any hint of civil twilight had begun to come into expression (Fig. 1).

A survey of the rather fragmentary literature bearing on the subject of the first morning song emphasizes the fact that observations have been too few and scattered throughout the long song season, in most instances, to give a reliable picture of the close trend of this dawn singing with the curves of twilight and sunrise. A single observation for any morning shows merely the order of singing of particular birds, but even here the actual magnitudes of separation from the twilight and sunrise

curves and from each other depend entirely upon the date. At or near the summer solstice the widest divergences appear to obtain, while at the end of the nesting season the birds may show a rapid closing in upon the time of actual sunrise in their singing activities.

Wright (1912 and 1913) and F. H. Allen (1913) have given averages of the time of singing for the different birds for their respective data. This has naturally led to some confusion and misunderstanding, for an average, from the nature of the relationship with the sunrise curve, may be very misleading. Allen (1913) took exception to some of the observations of Wright with respect to the order of singing of certain birds, and could not always make his average time of singing agree with the average as found by Wright. This is to be expected, for an average tells a very imperfect story of the nice relations between the civil twilight or the sunrise curve and the time of the first singing. Whether or not one's observations are taken on the spring side or on the fall side of the summer solstice or at the summer solstice itself is of vital moment in a clear understanding of the matter. A few days' difference in the period of the observations of different observers may produce marked discrepancies in their averaged times of the day when heard. Furthermore, my own observations show such a close correlation with the curves of twilight and sunrise that the matter of accurate position with respect to latitude and longitude must be taken into careful consideration. Not only must it be expected that the birds will sing progressively earlier with the higher degrees of latitude, since exact relations obtain with the sun's relative position in the skies, but in presenting these data attention must be given to correct standards of time as dependent upon the position of a given place in longitude upon the parallel of latitude in question. It is no simple problem to get at the laws of the true relations of the first activities of the birds with the eternally shifting conditions of the dawn. There is of necessity no direct relation between the time

of first singing of the birds of the Washington region, north latitude 38° 55′ 14″, and the same birds at Boston, Massachusetts, north latitude 42° 21′ 28″. There is, however, a direct relation for every parallel of latitude, for the birds begin and close their day with the astronomical position and movements of the sun throughout the year.

During the nesting season the bird population in a particular locality remains strikingly constant. Not only do the same birds sing, but many of these have their particular singing and roosting trees, to which they may repair with remarkable regularity, often times. Throughout the entire summer of 1929 during which my own observations were made, one house-wren roosted in the same tree just west of my neighbor's house. From this tree each dawn I was sure to hear his first song. He usually remained here singing persistently for some time even after the first song was delivered. Another wren always roosted in a tree in my garden. A redbird has roosted winter and summer in the same plum-tree in my back yard.

My own data as presented in this paper have been derived for the most part or perhaps entirely from the song habits of a stationary bird population, since the majority appeared to have their nests in the immediate locality. The following relations have obtained for the birds named below:

Song-sparrows—Several singing males around my garden.
Chipping-sparrows—Two at least.
Kingbird—The same bird for most of the period.
Wood-thrush—Several.
Wood-pewee—Two birds.
Robin—Several.
Catbird—Several.
Whippoorwill—Several.
Thrasher—One, and perhaps two.
Redbird—Two to three.
White-throated sparrow—Several.
Mourning dove—Several.
House-wren—Two, most of the time.
Maryland yellow throat—Probably the same bird most of the period.

It is probable that for any given season the same bird in a particular roosting place will afford a smoother

curve than several birds having more or less different physiological sensitivities and roosting in localities having different exposures to the sky. However, over a long

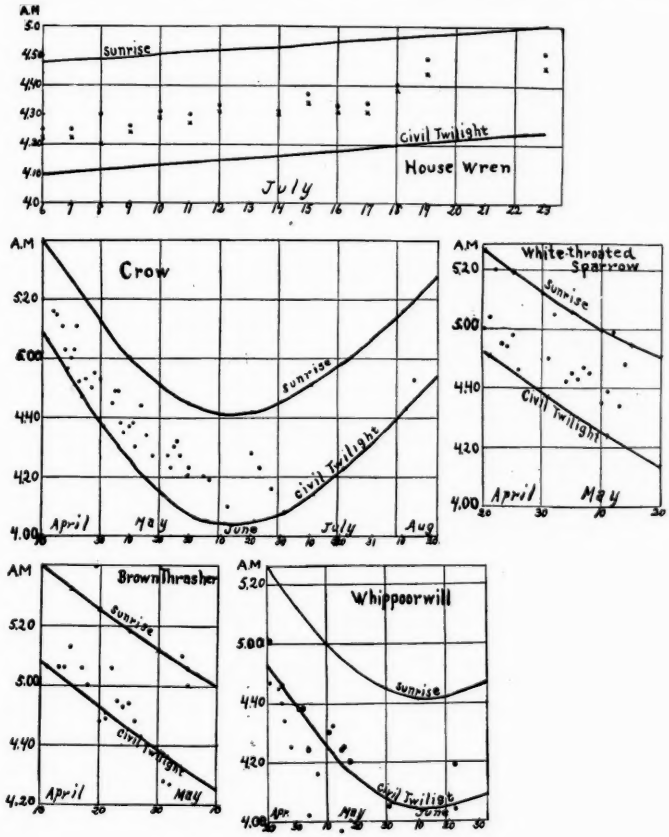

FIG. 2

First calls or songs of the House-wren, Crow, White-throated Sparrow, Brown Thrasher and Whippoorwill.

Records for the House-wren from July 6 to July 23, 1929, represent two individuals, and show the consistent earlier singing of one individual represented by dots, the first song of the other being represented by crosses. In the case of the Whippoorwill, the dots represent the beginning of the morning song period; the circles represent the last of this period.

period of years these data would tend to smooth themselves until they represented the average curve of the species for that locality. It is indicated that some individuals habitually sing a few minutes earlier each day than others, but as the facts stand at present this might

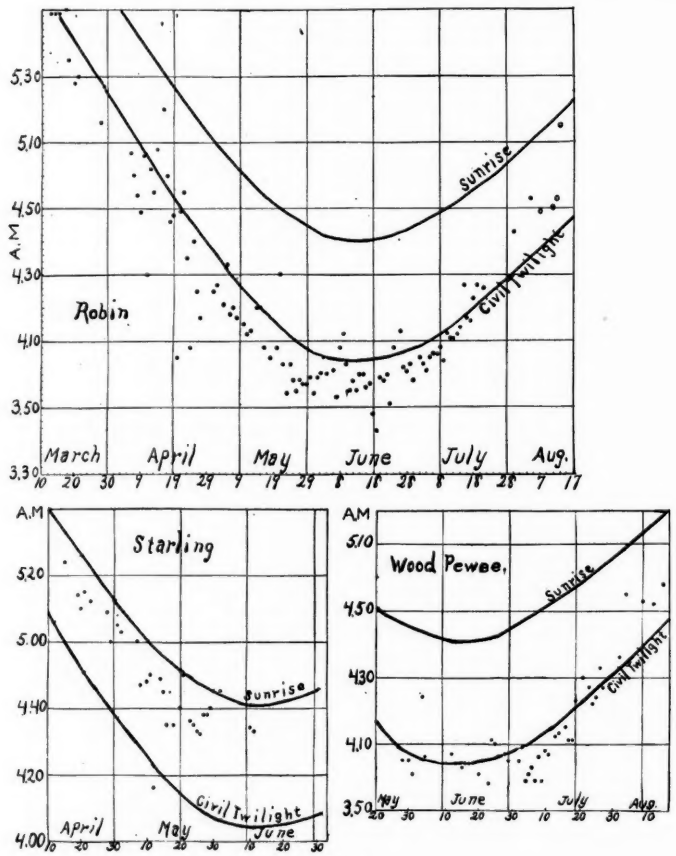

FIG. 3

First morning songs of the Robin and Wood-pewee and first calls of the Starlings visiting their breeding boxes at dawn. In the case of the Robin, circles in August represent calls, since at this time the song season is practically ended.

be due to differences in physiological sensitivity, or to differences in the conditions of the location with respect to the sky exposure. The time of singing for two house-wrens in Fig. 2 indicates relations of this nature.

For the most part, my own results indicate the same trends with those of Wright and Allen, more especially with respect to the order of singing of the several birds. The observations of Wright (1913) at Jefferson Highlands, New Hampshire, indicated that the song-sparrow and the chipping-sparrow sang earlier than the robin. Allen (1913) took exception to this, and claimed that for

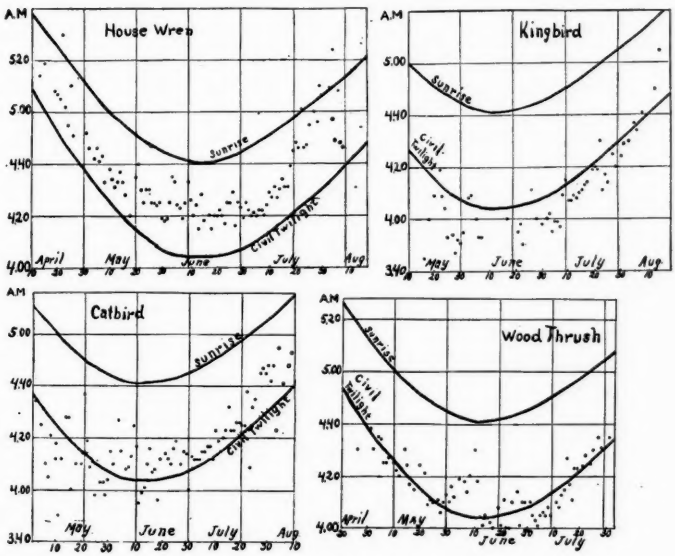

FIG. 4

First morning songs of the House-wren, Kingbird, Catbird and Wood-thrush. Circles in August represent call notes heard after the song season had ended.

his period of observations from May 29 to July 26 there was no time when the chipping-sparrow began before the robin, and but once when the song-sparrow preceded this bird.

My own data as presented in Fig. 6 showing the observations reduced to straight line trends by the method of least squares on either side of the summer solstice, June 19, indicate that the order of singing is not an invariable relationship throughout the season. In agreement with

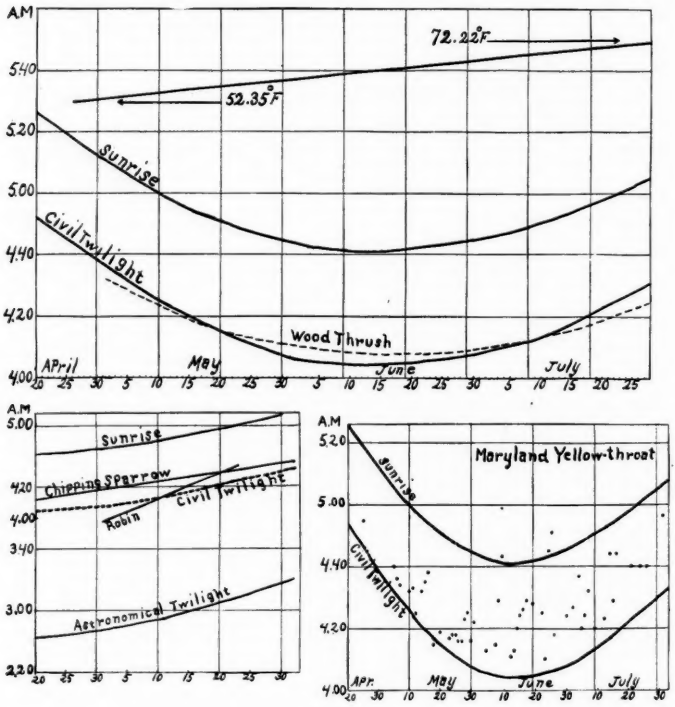

FIG. 5

First morning singing of some Washington, D. C., birds.

The earliest singing records of the Wood-thrush from April 26 to July 31, 1929, have been fitted to a curve of the second degree parabolic type of the potential series, to show the close relation with the sunrise and civil twilight curves through the period of the summer solstice. The straight line represents the temperature at the actual time of singing each day for the same period fitted to a straight line trend. It is evident that the time of singing is closely correlated with the curve of civil twilight. Singing records of the Chipping-sparrow and Robin are shown for the period June 20 to July 30, 1929, at Washington, D. C., reduced to straight line trends by the method of least squares.

Allen I have found the kingbird a consistently early singer, its singing preceding and trending with the civil twilight curve with remarkable constancy on either side of the summer solstice. Throughout May to near the middle of July the song-sparrow showed a wide scattering of very early records much preceding the more even trend of the kingbird. However, apparent differences in the order of singing of the birds in question as studied by Wright and Allen can not be taken too seriously until much more complete data have been accumulated for each period of the song season preceding and following the summer solstice.

My own data reveal striking differences in the order of singing of the various birds. Furthermore, some birds as the wood-thrush, the house-wren, the kingbird and the chipping-sparrow follow the sunrise and the civil twilight curves with remarkable regularity. The wood-thrush initiates its singing activities in almost perfect accord with the beginning of civil twilight as defined by Flammarion (1893), Folie (1893), Kimball (1916) and others, the sun at that time being 6° below the horizon (see Figs. 4, 5 and 6).

Before the summer solstice the house-wren follows a strikingly constant trend twelve to fifteen minutes after the beginnings of civil twilight, while the kingbird for this period tends consistently to sing from fifteen to twenty minutes before civil twilight begins.

The song-sparrow, the robin and the redbird afford the earliest records, and the trend from early spring to the solstice is one diverging steadily from the civil twilight curve in the case of the song-sparrow. From the data it would appear that during the height of the nesting and song season on the spring side of the solstice this bird is in some manner remarkably sensitive to some phase of the phenomena of astronomical twilight, for its earliest singing in May and June has always been consistently within this region between the beginnings of astronomical twilight and civil twilight. The trend of singing for

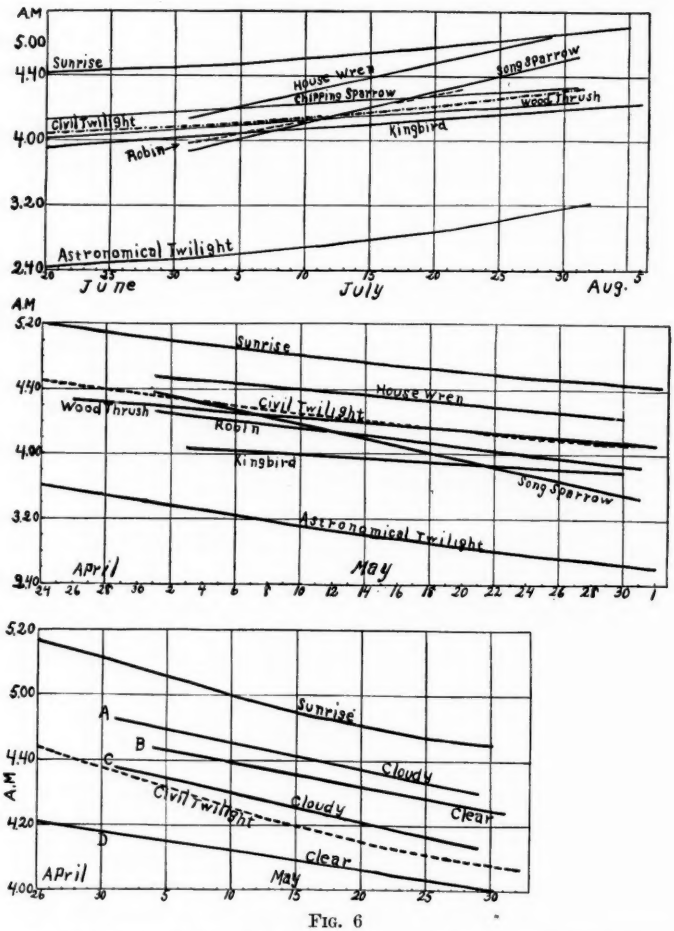

FIG. 6

Singing records of some common Washington birds before the summer solstice when the days are increasing in length, and after the summer solstice when the days are decreasing in length, reduced to straight line trends by the method of least squares. During the period June to August, the singing of the House-wren trended strongly into the sunrise curve when singing had about ceased in late July. The Kingbird was constant until singing ceased in August. The Song-sparrow showed a trend parallel with that of the House-wren.

Singing records for clear and cloudy mornings, April to May, are shown reduced to straight line trends by the method of least squares. A and B represent the House-wren; C and D the Wood-thrush.

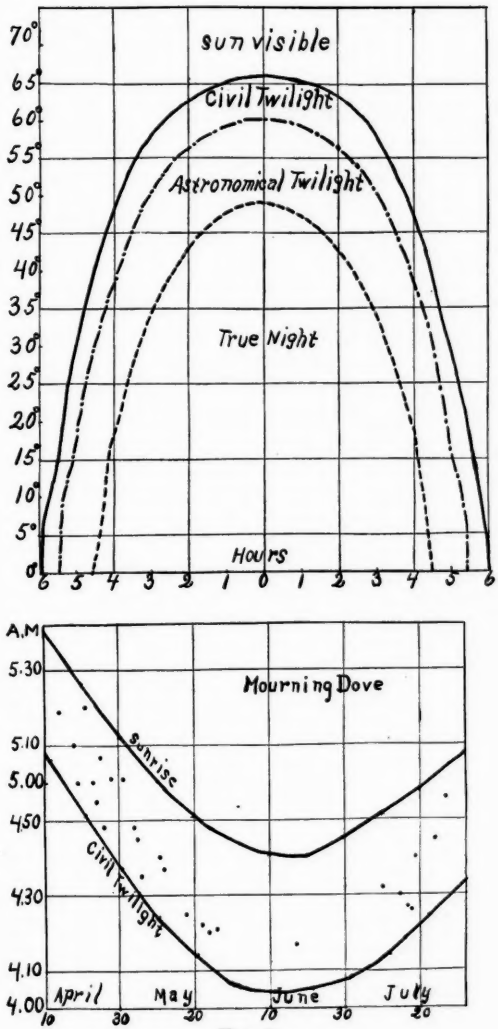

FIG. 7

Records of the first morning notes of the Mourning Dove April to July. Diagram showing the time elapsing between sunset and sunrise for different latitudes, the periods of duration of civil and astronomical twilight at the time of the summer solstice June 21. In a study of the dawn singing of birds, records falling within the period of true night can safely be discarded as having no relation to the beginnings of astronomical twilight which is the first indication of coming dawn.

this period appears to be correlated with some expression of astronomical twilight, for it extends far below the beginnings of civil twilight. There appears to be a rather wide scattering through June for the robin, the redbird and more especially for the song-sparrow. However, since these earliest song records are always well within the zone of astronomical twilight, they must be regarded as song expressions in some manner actually associated with phenomena of approaching day which they have been able to appreciate, however low the light values may appear to be.

The earliest singing of the birds is often times of a very distinctive nature. In the case of the robin and the wood-thrush, the first signs of morning activity may be expressed by a few querulous call notes, although this is no invariable rule. These birds begin singing almost simultaneously following the first notes of the species. This prompt and simultaneous singing appears to be rather an individual response to the same influences of the dawn than the result of social stimulation of one bird upon another in the species group of the locality. This is indicated from the fact that an individual house-wren roosting always in a particular tree invariably sang a few minutes later each day than another individual not far away. Of two wood-pewees singing near by one rather consistently sang earlier than the other.

The song-sparrow and the redbird were more erratic in their singing behavior than any other species, the first song often being followed by a long pause before another was delivered by the same individual. As the dawn advanced, however, others introduced their songs followed by continuous singing by the group, often times with striking suddenness.

The data reveal a number of significant relations and correlations. It is evident that each species of bird has its established place in the order of singing for a given period of the season, although the relations may change markedly toward the end of the nesting and song season.

It is obvious that some birds begin their dawn singing at or after the beginning of civil twilight, while others wait until the light conditions have advanced well toward actual sunrise. It is plainly to be seen that a number, prominent among these the kingbird, are able to appreciate the beginnings of the dawn considerably below the beginnings of sky phenomena attending civil twilight.

The questions now arise as to how the birds awaken and how their nervous organizations respond to particular phases of astronomical and civil twilight, as it would appear they must to maintain their relative position so precisely. Wright, Allen and others have termed it the "*morning awakening.*" I am inclined to believe we are somewhat in error here if we consider the first morning song an indication of the first awakening of the birds. The true sleep position of the birds is assumed when the head is tucked beneath the wing. In this position the eyes must be closed, and there is reason to believe that so long as this position is maintained the birds can not become aware visually of the weak twilight changes with the advance of the phenomena of dawn. This is borne out by tests which I have made with sleeping pet canaries. Once the head is tucked beneath the wings a strong spot light or electric light may be turned upon the bird without causing it to remove its head from its wings. I have performed the same test with a mother starling brooding its young in an observation box a few days after the hatching of the eggs. There is reason to believe that the birds have abandoned the true sleep position and are waiting alert for the coming of the dawn long before the first morning song is delivered. I look upon this first morning song, not as an indication of the first awakening, but as an indication of the first moods of expression to be followed as soon as light conditions admit by the next phase—actual physical activity in the direction of flight and search for food. This appears to hold more especially for the very early dawn singers such as the song-sparrow, the redbird and others. I have observed that

even the house-wren, singing its first song well after the beginning of civil twilight, may not leave its roosting tree for some time after its first song, but will continue to pour forth its phrases from the same position.

A number of birds, notably the wood-thrush, associate their song with striking precision with the beginnings of the civil twilight. Civil twilight as Europeans have understood it is not a purely arbitrary distinction, but one dependent upon definite phenomena attending positions of the sun below the horizon morning and evening. Its termination has always been of interest in the practical affairs of men working out of doors since it marks the time when such work must cease in the evening owing to darkness, if artificial illumination is not resorted to. Whether or not the wood-thrush has an eye somewhat similar to our own in its sensitivities is not known, yet we may say it begins the practical affairs of its economies like ourselves with the beginnings of civil twilight. However this may be, it is evident that civil twilight as we recognize it and as the wood-thrush recognizes it must afford something in common to the nervous organization of the bird and the human to follow the phenomena of its appearance so closely.

In his first paper Wright (1912) was inclined to believe that cloudiness did not delay the morning singing to any noticeable extent. My own observations, handled by more careful statistical methods, reducing the data to straight line trends for given periods, indicate without exception that cloudiness at dawn has a more or less decided effect in delaying the first song, as shown in Fig. 6 for the wood-thrush and house-wren. Witchell (1896, p. 64) has noted the sudden cessation of song by the birds in England with a passing cloud, and the instant resumption of singing with the return of sunshine. If the birds are at all sensitive to the low light values obtaining at early dawn, it would be rather anomalous if heavy cloudiness did not affect their responsiveness in one way or another.

With respect to the moon, Wright in his first paper (1912) considered moonlight without effect, but in his second paper (1913) he was inclined to give it more weight. His views were changed by a single observation during one morning with a brilliant full moon, when the birds sang earlier than usual. However, the question of the moon's light is quite unsolved so far as most birds are concerned. It may be stated, however, that even the true nocturnal birds are not lovers of absolute darkness, including the whippoorwills and others of the goatsucker family. These birds depend upon their visual powers to secure their insect prey, and if their eyes make use of the rays of the visible spectrum ranging from red to violet as we appreciate it, the presence of some light is absolutely essential in their nocturnal economies of feeding themselves and their young. On brilliant moonlight nights such birds are exceptionally active. These birds at other times are rather more crepuscular than strictly nocturnal in their habits and have more or less definite evening and morning periods of song, when their activities are associated with twilight illumination. The mocking-bird is undoubtedly aware of moonlight intensities during the height of the song season, for its wild rhapsodies amount to an all-night serenade on brilliant moonlight nights. I am of the opinion that this is of the nature of twilight singing, and that the mocking-bird is perhaps fooled into regarding the moonlight conditions as a sort of twilight or dawn light. My own data are insufficient to throw any light on the influence of moonlight on the first dawn songs. The matter of normal light intensities during the oncoming of the twilight periods is anything but constant, and it is probably a rare event to secure the maximum brightness of a perfectly clear day as a basis for comparison. In the case of Wright's instance of early singing, the brilliance of the moonlight may have been supplemented by an exceptionally brilliant twilight attending an unusually clear sky, which in itself would tend to throw the intensity values of the

illumination much ahead of the average condition and perhaps influence the first singing of the birds in a positive way.

On the morning of August 26, 1929, which was attended with very clear sky conditions and a brilliant moon, both the redbird and the catbird began their querulous *pit–pit–pit* and *skat–t–t–t* and *scare,* respectively, much earlier than usual. The former delivered them at 3:58 and the latter at 4:00 A. M. There was then a long period of silence until 5:00 A. M. for both birds, when the true dawn calling as it seemed was resumed. The brilliant moonlight may have stimulated this exceptionally early mood of expression for the time of the year, but if it did the birds appeared to decide that the true dawn had not come after all, and later delivered their true dawn notes to the exact schedule. Whether these instances are due to the influence of the moonlight can not be decided until many more systematic observations have been accumulated.

The early dawn singing of most birds is usually more or less distinctive in its character and manner of delivery. The bluebird, one of the very early risers, singing around 4:00 A. M. in early July, delivers its warbling phrases very hurriedly for the brief time during which it sings. The red-eyed vireo often sings hurriedly. The kingbird, in keeping with most of the flycatchers, has very characteristic habits of dawn expression which have been described by Olive Thorne Miller (1897, p. 14) and Leon Augustus Hausman (1925).

The wood-pewee, however, among our eastern birds has evolved a strictly specialized twilight composition. This appears to have been first noted as distinctive for the early morning and evening twilight conditions by that able field naturalist, Henry Oldys (1892 and 1904). So marvelous is this song in its phrasing and rhythmic repetitions that Oldys regarded it as second to no form of bird expression in technical rank. My own data are based upon these expressions of the wood-pewee, and it

is evident from the nice correlation with the curve of civil twilight that it is a specialized song associated with a narrow range of illumination conditions occurring at this time (see Fig. 3). The duration of this distinctive repetitive song is around twenty to twenty-five minutes, and it is concluded when light intensities have reached a certain higher value, apparently as definite in its level as the lower level at which the song began.

The dawn song of the birds is always more distinctively enthusiastic than the evening renditions. Furthermore, the same relations with the twilight intensities are not so nicely observed at the closing of the day, the birds often ceasing their expressions relatively earlier with respect to the time of sunset than they begin them with respect to sunrise, although this is not an invariable rule. On July 17, with clear skies, the wood-thrush sang forty-four minutes before sunrise, and only till thirty-three minutes after sunset. It is possible that fatigue comes in as a prominent physiological condition at the close of a long hot day of intense activity concerned with the sustenance of their nestlings and themselves.

If the birds adjust their activities so nicely to particular obtaining light conditions harmonizing with their physiological requirements one is given to wonder concerning the effects of weak artificial illumination upon them at night. It is evident from casual observation that the street lights of our towns and cities appear to exert little effect upon the activities of the birds. The sparrows and doves retire to roost almost beneath them, and the starlings may even roost upon them in a state of suspended activity until the dawn of another day returns. A house-wren roosted in my neighbor's tree beside his windows, and within the rays of a street light near by, retiring and arising at the usual time. I have tested a roosting redbird in my garden many times with the powerful rays of a large spot-light full in its eyes from a distance of only a few feet, but it merely sat and blinked with quizzical mien. It is possible that the point effect

of the light is appreciated as an abnormal condition. A powerful diffuse light of the proper intensity and quality might tell another story so far as the dawn singing of a bird is concerned.

From the preceding discussion and data it is evident that the birds are highly specific in their responses to particular illumination conditions of the dawn. The first morning singing is a highly orderly procedure for the different species. At the height of the song season the order of singing for any particular period is strikingly regular and appears to be associated with very definite illumination values attending certain phases of expression of the phenomena of astronomical and civil twilight. The temperature relations appear to play a very minor part, since the trend of the curve of singing from January to June is consistently earlier each day, while the temperature curve from spring until August shows a regular trend upward in an inverse way.

The summer solstice affords a nice turning-point for the determination of positive correlations between the first dawn singing of the birds and the swing of the twilight, sunrise and temperature relations. In the case of the wood-thrush I have expressed the data of the earliest songs for the singing period of April, May, June and July as a curve of the potential series of the second degree parabolic type, since a straight line is quite inadequate to express the relations obtaining with the sunrise curve through the solstice period. It will be seen from Fig. 5 that this curve follows with striking agreement the beginnings of civil twilight, which is a fixed function of the sunrise. To make more convincing the lack of correlation of this curve of singing with the curve of the seasonal temperature swing, I have for the same period reduced the actual temperatures when the songs were heard at dawn to a straight line trend. At a glance it will be seen that the correlations are entirely with the civil twilight and sunrise curves.

What is the physiological mechanism of these specific sensitivities to the various phases of the dawn twilight? One can not well think of it as anything but a visual impression, but visual or retinal sensitivity depends upon deep and vital physiological functions. The true season of song is associated more especially with the mating season, and it is well known that the bird's physiology undergoes marked changes preceding the mating season and following the close of this period. The sexual organs, ovary and testis, normally become awakened to conditions of intense reproductive functioning in springtime with a profound decline of active functioning following the end of the nesting season. Coincident with this summation of intense physiological activity of the entire reproductive system in spring are the behaviors of mating, nesting and singing, leading to or attending the successful raising of the family. Following the midsummer period, the reproductive energies rapidly wane, family life is no longer an issue, song generally ceases and the birds are reduced to a mere nutritive condition of physiology. Profound changes have taken place in the entire sexual system. The testes have become reduced in size and profoundly quiescent in their functions.

In the main, song is a function of intense sexual activity. It can be seen from the data presented that the singing curve indicates different degrees of sensitivity to the dawn influences, as in the case of the song-sparrow. Long before the midsummer solstice, the robin, the redbird and the song-sparrow gave evidence of hypertension in their singing moods. They showed a marked trend toward earlier rising until the solstice was reached, when a gradual decline set in. It would appear that sensitivity to the earlier influences of the dawn had increased up to the solstice, with a more or less rapid decrease in this condition after the solstice. So marked was this for some species that some of the birds in August actually withheld singing until near or even after sunrise. The robin, house-wren, redbird and song-sparrow were among these. Finally, singing practically ceased for the

majority of species, to be replaced by various call notes. What the physiological factors are which determine and govern these upward and downward trends of sensitivity in the morning singing can not at present be stated. It is possible that certain hormones associated with the intense activities of the testes may render the nervous organization of the birds highly sensitive to particular light conditions obtaining during the dawn twilight. At the present time physiologists can offer nothing but conjecture on this point, however.

To say the least, it is evident that the birds are attempting to sing on remarkably fine schedules established by some response of their nervous organizations to the influences of the dawn. It is indicated that the house-wren is maintaining a singing relation with respect to conditions of light much closer to actual sunrise than the kingbird. If it is a matter of light intensity, the singing reflex of the kingbird is consistently far more sensitive than the wren's to some phase of the dawn light which it is able to perceive. As determined by Kimball (1916, table V, p. 620) the sky light at sunrise or sunset on clear days may approximate 33 foot-candles. At the end of civil twilight this may approximate around .4 foot-candle. Zenithal full moon is given as approximating .02 foot-candle. Kimball in table VI gives some interesting figures showing that the twilight illumination exceeds the illumination of the zenithal full moon until the sun's center is about 8° 40′ below the horizon. This position of the sun at the summer solstice occurs between forty-nine and fifty-one minutes after sunset or before sunrise. At this time my data show the kingbird delivering its first song as early as 3:50 A. M., the range running to 4:00 A. M. or forty-two to fifty minutes before sunrise. Around the middle of May there were records even earlier than this. As far as published records afford adequate photometric data this would indicate that the kingbird tends to deliver its dawn song close to those limits where zenithal full moon and the twilight intensity are about equal in value, that is, approximating .02 foot-candle. This is approxi-

mately one twentieth the value .4 foot-candle, which marks the beginning of civil twilight, near which my data show the wood-thrush holding the trend of its earliest singing. The little house-wren at the summer solstice apparently holding its singing near an illumination value of 3 to 4 foot-candles is awaiting an intensity 150 to 200 times as strong as that which excites the kingbird into song expression.[3] The song-sparrow at the beginning of June shows a far greater sensitivity than this, for its trend of earliest singing when reduced to a straight line value by the method of least squares crosses that of the kingbird and remains below it well into June. None of the birds which I have observed have approached so near the beginnings of astronomical twilight as the song-sparrow. Yet one must conclude that some phase of its phenomena has been perceived by these sparrows, since in every instance the earliest and most sporadic records have come within the limits of this early phase of the oncoming dawn day after day. It would appear that the light intensities of these early records for the song-sparrow must be even less than one tenth the intensity level at which the kingbird is stimulated into song expression. This would indicate a value as low at least as .002 foot-candles which the birds had perceived as presaging the coming of dawn. This, however, would depend upon whether the bird were perceiving the average diffuse values of sky light from its position, or were directing its eye to the east to receive the strongest light at more or less normal incidence.

To my mind there is nothing unreasonable in these specific gradations of light appreciation as indicated by the different birds. It would appear that the chimney-swift and others beginning their activities at or near the time of actual sunrise represent one extreme of sensitiv-

[3] These figures are based upon Kimball's chart Fig. 1, p. 619, *Monthly Weather Review*, Vol. 44, showing average zenithal light conditions for civil twilight, the duration of which during April, May and June is about thirty minutes. This would give about five-minute periods for each degree. There is great need for careful photometric data in these singing relations.

ity, while the Caprimulgidae, including the whippoorwills, represent the other extreme, since they are birds which can pursue their usual economies at very low light intensity levels. During the height of the nesting season the mocking-bird possesses some of the characteristics of the strictly diurnal birds and the strictly nocturnal species. The kingbird and the song-sparrow represent intermediate types, seasonally, since they are highly crepuscular in their song habits during the nesting season.

It is indicated that our distinctions between the nocturnal, the crepuscular and the more diurnal birds are only matters of degree. Mere disappearance of the sun below the horizon does not constitute true night. The presence of appreciable twilight merely adds to the length of the day. There is a dawn period of illumination near the beginnings of civil twilight when the day and the night birds are on common ground, and during this period the voice of the whippoorwill mingles with the notes of the kingbird, the robin, the wood-thrush and the wood-pewee. Advance this period into the day or push it backward into the night time, and the strictly nocturnal birds and many of our diurnal birds would project their song activities into this period. This is just what happens in far northern latitudes, where a common twilight finally joins night with day. The disappearance of the sun below the horizon at the latitude of 50° does not constitute true night but in a sense a continuous twilight period from June 2 to July 12. As the pole is approached beyond this latitude the twilight period becomes more prolonged with higher intensities until a point is reached where the sun remains visible above the horizon for a certain period.

It is not to be wondered at that the birds should respond to this continuous dawn light just as they respond to the shorter durations definitely preceding and closing the summer days in lower latitudes. It has always seemed to me that many of the birds of New England sang more persistently at night than farther southward. At the time my observations were made, however, I knew

nothing of the long twilight periods of midsummer in that region, extending near 10 o'clock P. M. and beginning at 2 A. M., leaving only about four hours of true night. When southern Canada is reached, near the parallel 50, one should in midsummer naturally expect to find much more apparent night singing, other conditions being equal, than in far southern latitudes of the South Carolina or Florida region.

From the data presented it is evident that the birds at certain periods during the mating season become highly sensitive to the influences of the coming day. In a sense it would appear that their visual organization behaves as a very sensitive photometer, appreciating very low light intensities upon which definite forms of expression are based, one of these being the first vocal expression of the morning. Since cloudiness at dawn tends to delay more or less appreciably the delivery of the first song, I am inclined to believe that the intensity of the light of the visible spectrum operates upon the visual organization to cause the birds, each with its own sensitivity, to strike the minute approximately at which its mechanism is set.

One is given to wonder what relationship there is between this behavior of the birds and the matter of the migration impulses. To say the least, there are weird analogies. In the case of the first morning song, the birds adjust their singing with remarkable constancy and precision to the variable time of sunrise, backward toward midnight until near the summer solstice, and forward when the summer solstice is passed.

In the case of the great migratory movements, the birds appear to follow the sun, to become restless and turn with the sun at the summer solstice, as if in some manner their physiological mechanisms were mechanistically synchronized with this dominant celestial phenomenon upon which the swing of the seasons depends. During the height of the migration urge, there is an actual speeding up of the northward spring migration as the higher latitudes are approached, until some species

project themselves with almost foolhardy haste ahead of the advancing isotherms into regions of cold and snow, oftentimes with disastrous results.

Furthermore, just as different species of birds in their dawn singing appear to be specifically sensitized physiologically to particular intensity levels or to other factors of the twilight, we have in the migration movements the same constancies of relative position in the time of arrival in spring and the departure in autumn. It would appear as if the birds each in its own way were awaiting a certain stimulus before the urge to migrate could assert itself. Nothing is more patent than this order of migratory coming and going with the birds; a similar fixity of order prevails in their first dawn singing.

While it is plain enough that the birds are definitely responding to some influence of light coming into expression with the twilight phenomena at dawn, it is not so easy to determine the mechanism by which the birds are led northward and southward with the seasonal movements of the sun. Singing at dawn is a mood of sedentary expression while remaining *in situ;* migration is a matter of positive directive orientation toward and from certain points. Light intensity appears to govern the singing impulses and the localized activities attending the summer home life. I can not see how light intensities or changes in day length in themselves can orient the birds definitely anywhere. I can conceive of tropistic responses connected with northward and southward movements of the sun to which the birds may respond with mechanistic exactness, just as a sunflower follows the sun in its easterly-westerly course. It is evident that we know very little of the finer physiological potentialities and adjustments of the birds or any other creatures to light or to other factors of the usual environment.

We may say without hesitancy that the birds possess a physiological mechanism that is attuned with extreme nicety to changes in the length of the day at whatever latitude they may make their home. If changes in the

actual length of day in some manner affect their nutritive and reproductive cycles, the sensitivity of their physiological mechanism through some operation of the visual sense would appear sufficient to record these changes.

The behavior of the birds in their first dawn singing is a fascinating one. There is a broad field here for much research at different latitudes from the equator to the poles. Data carefully secured with respect to the intensity values of the different phases of civil and astronomical twilight should yield very interesting correlations. Provided there have been no changes in specific sensitivity, the members of the species in the higher latitudes should sing progressively earlier until the region of continuous twilight is reached.

W. W. Cooke, one of the leading authorities on the subject of bird migration, once wrote (1910, p. 386), "Were the surface of the earth level and the climate absolutely uniform, birds would arrive at a given place on approximately the same day each year."

With respect to the first dawn song at the height of the song season I am inclined to say that were there no changes in the conditions of the skies or the weather, the illumination values remaining at their maximum for each day and the birds so situated in their roosting places as to enjoy the same intensities at dawn, they would tend to behave as extremely accurate chronometers, recording each day for each year the approximate time within the minute. As a matter of fact, such accuracy can not be expected, since our records both for migration data and for the first songs of the dawn are eternally the results of two omnipresent and interblending averages, the one an average of the conditions of environment, the other an average of the physiological constancy of the species. I would affirm both as to the dates of migration and the time of singing that were the species assemblage reduced to its purest physiological conditions, the precision of the data would be greatly enhanced. Even as matters stand with these individual and environmental variables enter-

ing into our field data, the correlations are remarkably constant. These critical features of the two behaviors, the migratory exactness and the exactness of the timing of the first morning songs, make me feel that somewhere, somehow, the sun and its light which is known to govern the morning singing must regulate the orientations and precisions of the great, world-wide migratory movements.

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SHORTER ARTICLES AND DISCUSSION

CAN SEX RATIO BE ALTERED IN DIOECIOUS PLANTS?

Introduction

Since recent years numerous publications concerning the sex in asparagus (which is normally dioecious) have appeared in biological literature. These researches have not only a great influence on some phase or phases of evolution, but also possible application on the practical end of the development of asparagus industry. Since it has been experimentally found by Tiedjens (1924), Green (1890), Thompson (1923), Böttner (1921), Robbins and Jones (1925, 1926, 1928) that staminate plants produce more spears and greater weight of spears than the pistillate plants, it was necessary to secure staminate plants in order to gain greater returns.

In nature the staminate asparagus plants are fewer in number, while the pistillate (less desirable) predominate. This was shown by the writer during 1926 on 17,000 acres of asparagus. For instance, it was found, based on 34,040 Mary Washington and 7,629 Palmetto (the two most important varieties of asparagus) plants, that the former had 28.9 per cent. staminate, 60.1 per cent. pistillate and 11.0 per cent. non-blooming plants, while the latter had 33.1 per cent. staminate, 58.5 per cent. pistillate and 8.4 per cent. non-blooming plants during the first year. There are many other authors, such as Babcock and Clausen (1927), Goldschmidt (1920), King and Stolzenburg (1915) and King (1918), who have shown that the sex ratio is unequal and that many conditions may modify it. Furthermore, Hertwig (1905, 1907), Miss King (1918) and Loeb (1892) have shown rather distinctly that sex ratio has no fixed value.

In order to change the usual sex ratio in asparagus, the writer carried an extensive series of experiments at Montezuma Ranch, owned by the California Packing Corporation, at Rio Vista, California. Since the methods and the information seem to be of interest to biologists in general and evolutionists in particular, it is hoped that this short summary will be of some service in the elucidation of the mechanism of sex segregation.

Materials and Methods

Two classes of pollen grains were recognized as shown by Correns (1900) and Sears and Metcalf (1926). Matured pollen was collected from 800 Mary Washington asparagus plants, all grown under the same environmental conditions. The pollen was collected in small air-tight phials and divided into four lots. It was previously recognized that as the pollen gained in age, odor, presumably due to esters, essential oil or similar chemical volatile constituents, decreased.

Of the four original lots, lot A was further divided into three portions. Portion 1 was exposed for six hours, 2 for twelve hours, 3 for 24 hours. Pollen of lot B was used for distillation of the essential oil by steam following Houben's (1921) method, which was further distilled by Allen's method. The distillate was sprayed by means of a special apparatus (based on the principle of a simple nose and throat atomizer) for gentle spraying.

Pollen of lot C was divided into three portions, and three hanging drop slides were cleaned, cooled in desiccator and very carefully weighed to constant temperature. The pollen in these slides was increased in weight (by gently spraying the distillate) by 10 per cent., 30 per cent. and 60 per cent. of the original weights of the pollens. The slides were immediately covered and sealed with wax until pollination time.

Pollen of lot D was divided into three portions also, and these portions were treated exactly the same way as the pollen in lot C except that the pollen was sprayed with water instead of the distillate as previously used.

The pollen of lots A, C and D was used in pollinating 100 female asparagus plants of Mary Washington variety. Each plant contained six and eight flowers. The berries when matured by such pollination were picked and the seeds secured. These seeds were planted and the number of the male and female plants secured from each treatment was counted and the data analyzed by the approved statistical methods.

Discussion

The data (the details will shortly be published in the *Journal of Genetics*) seem to show that as the exposed period was increased from six to twenty-four hours the absolute number as well as percentage of staminate plants decreased while the pistillate plants increased. When the pollen was sprayed by vola-

tile oil (distillate, until the pollen gained 10 per cent. of its weight) the number as well as the percentage of pistillate plants decreased while staminate plants increased. The same happened for the other two portions of this lot.

The data also seemed to show that by varying the amount of water (to the same extent as for the distillate) the ratio between the staminate and the pistillate plants remained practically the same. Thus it would seem that spraying with distillate brings about some change or changes presumably physiological in the pollen. Such a changed pollen on fertilization of the egg may modify the chromosome equipment or gene balance to such an extent that factor or factors for maleness may be more favored than for femaleness. As the amount of the distillate is increased this favorable effect for male is also increased.

The chromosome equipment of the zygote, formed after the egg was fertilized by means of pollen treated with and without the volatile oil, has been followed throughout the course of the zygotic and the embryonic development. The study seems to indicate that the zygote resulting from the treated and non-treated pollen has considerable difference in the chromosome equipment. There seem to be sufficient data derived from this study, which shows that environmental factors affect the physiological activities of the pollen (at least in asparagus). This physiological effect in consequence has a direct bearing on the sex segregation by affecting the chromosome equipment. Our concept that chromosome equipment is not affected by ecological factors as emphasized by many workers seems to be questionable in the face of these experiments. Those who have already pointed out such a possibility gain evidence for their views from these researches.

The writer is well aware of the fact that the above said state may not apply to all cases. Not only that, but the results are not warranted until more data are obtained to this effect.

It is a pleasure to thank Professor E. B. Babcock, professor of genetics, University of California, for offering criticism when the results were presented in a genetic seminar at the said university in 1927.

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RADIATION AND GENETICS

THE extremely interesting paper by Professor Muller, in the May–June AMERICAN NATURALIST, suggests a few comments. As long ago as 1893[1] I called attention to the existence of "species-forming areas." In certain regions, wide-spread genera will show an exuberance of species, no particular reason being evident. We may now add that there have also been "species-forming periods." Thus, the dipterous genus *Plecia*, now represented by few species, was very rich in species during Tertiary time, while the genus *Tipula*, also exuberant during the Tertiary, remains equally so to-day. The bee genus *Heriades* is richly represented in South Africa, but has few species in Colorado. Yet in Miocene times there were many species in Colorado. Contemplation of these and many similar facts shows that excessive multiplication of species has been characteristic of no particular time or place, one genus showing it here or now, another there or formerly. There has apparently been no set of physical conditions which has produced rapid evolution all along the line, unless we consider the matter in terms of geological epochs, and broad climatic changes such as occurred in the Permian. Such modifications of life as characterize geological epochs can well be attributed to ordinary Darwinian agencies.

However, the rate of evolution in different groups differs exceedingly. As Dr. Matthew has recently shown, the dog family (Canidae) has undergone great changes since the Miocene, all the genera having changed. Yet the flowering plants of the Miocene are congeneric with those of to-day, and many of the species are closely allied. There has been no progressive evolution of the flora since the Miocene, so far as the records show. The Miocene insects are also essentially "modern"; and when, as in the Bombyliidae (Diptera) we find a long series of extinct genera, they are not the ancestors of the common genera of to-day, which came in from elsewhere and supplanted them.

It has recently been shown by Fernald that the areas in northwestern America which were unglaciated during the last (Wisconsin) great glaciation support a flora which apparently survives hardly or not changed from the Pleistocene. This is particularly true of Newfoundland, where also the little Rocky Mountain snail *Vertigo coloradensis* survives unmodified, as

[1] *Trans. Amer. Entomological Society*, 20: 321.

lately reported by Vanatta. The general outcome is that genera and species, under normal conditions, are extraordinarily persistent, and the slow process of evolution indicates a resistance to change in the living genes which is really marvelous.

Dr. O. C. Lester has published a report[2] on the radioactive properties of the mineral springs of Colorado. It appears that the waters at Springdale, in Boulder County, are the most highly radioactive in the state. Both the water and gas are very much more active than in any other locality examined.[3] On account of this condition, I recently undertook to collect the plants and invertebrate animals of the locality, to see whether they would present any unusual features. So far, the collecting done has amounted to little, and what we have has only in part been worked out. The most interesting plant obtained is the wild tobacco, *Nicotiana attenuata* Torrey. Professor R. E. Clausen reports of the material: "I am unable to detect anything but minor differences between them and the type of *N. attenuata* which we have grown here." A grass, *Elymus canadensis* L., is reported by Mrs. A. Chase as "depauperate." Among animals, a diplopod, *Parajulus venustus* Wood, is reported by Professor R. V. Chamberlin as "variant in gonopod." A small gelechiid moth is said by Mr. A. Busck to represent a new species. Various other species of plants and animals appear to be quite ordinary. I do not attach any importance to these findings, and am not confident that it will be possible to detect any positive results of the radiation in the biota. For one thing, new physical determinations are needed; thus we do not know the condition of the air in the canyon. If a positive, viable and effective mutation in some species (probably affecting a number of individuals) is produced every ten or every fifty years, the results in course of time will be considerable. But one would have to collect the mutated species before it spread over the surrounding country, or crossed with the more normal form, giving rise presumably to generally increased variability. Thus there would be many difficulties in the way of tracing the changes to their original source, supposing the radioactivity to have been an effective cause.

There is, however, apparently good reason for considering that there is likely to be more radioactivity in caves than in the

[2] Colorado Geological Survey Bulletin, No. 11, 1920.

[3] See numbers 207–210, on p. 182.

open. It is not impossible that the peculiarities of cave faunas may be at least in part due to this cause. Take such a cave-beetle as *Aphaenops pluto* Dieck, with greatly elongated antennae, legs and bristles. One has the impression that the metabolic balance has been upset and this might result from radiation. The various modifications of cave animals, often seemingly purposeless or without value for the organisms, might be due to such causes. In an irresponsible moment we may even speculate whether the grotesque facial structures of bats, commonly inhabitants of caves, have any such origin.

All these matters take on a new aspect in view of Vernadsky's findings of radium concentration in living organisms. He seems to have used only plants and aquatic invertebrates—those creatures which in nature are especially stable. It now remains to be seen whether there is any relation between the power of radium concentration and the variation or evolution of the organism. Thus, some moths are excessively variable; others, not distantly related, extremely constant. Mammals are, or have been, evolving very much faster than plants or invertebrates. Can we say that for effective variability we need a certain ability to accumulate radium (or radioactive materials), plus a susceptibility to its influence, both being variables, resulting in diverse consequences under identical physical conditions?

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OBSERVATIONS ON MATERNAL INSTINCTS OF BIRDS

A FEW years ago, while spending my vacation collecting popular sayings for a report on folk-lore, I was surprised by some statements of country children concerning the maternal instincts or rather the caprices of birds. They claimed that when somebody touches, even though with only the tip of his finger, an egg in a bird's nest, either before or during incubation and even when the mother bird does not see anything, the latter leaves the nest for good. Nay, more, with some species of birds, as for example goldfinch, looking at the eggs would be sufficient to cause the parents to leave their nest.

These statements and some others concerning the magical effect on birds of the gaze of reptiles, although belonging for the

most part to pure folk-lore, induced me to seize such opportunities as might occur of observing the reasons why a bird abandons its nest.

Here are the observations and experiments I made. They concern the sparrows, the warblers and the blackbirds, which are very numerous in Switzerland (Fribourg and Geneva), the country in which I experimented.

I. A nest of warblers was built in a bush, at the height of the eyes. I purposed to find out how much my visits displeased the birds, so I proceeded in the following way. I approached slowly and without noise to the nest, at a time when one of the parents was brooding. It was motionless and its eyes were steady. Then I came nearer. When I was at a distance of half a yard it showed signs of nervousness, moving its head rapidly and blinking its eyes. I came still nearer. Then it flew away without the least noise or cry. I repeated this experiment sixteen times, that is, once or twice a day during the brooding period. On the sixteen experiments I found the male on the nest five times and the female eleven times. They did not abandon the nest at all. The little ones were hatched normally.

II. There were many sparrows' nests in the projecting roof of a house where I was living. Two of them, about twenty feet apart, were at the beginning of the incubation period. One contained very small eggs and the other considerably bigger ones, so that at first sight the difference between them was striking. As I could easily reach the nest by the garret of the house, opportunities for the observation were most favorable. I chased the birds out of their nests by walking noisily near by, and then I took one egg from one of the nests and exchanged it for one from the other nest. The two sparrows came and, without giving any sign of uneasiness, continued brooding, each in its own nest, as if nothing abnormal had taken place. All eggs were hatched in due time and the little ones were nourished indiscriminately by their own or their adopted mother.

III. The nest of the warbler of which I spoke first contained only three eggs at the time when I found it. I took one of them, stained it red with a strong eosin solution, so that it was very different from the two others, and returned it to the nest. This did not frighten the mother bird in any way; she came and laid her fourth and fifth egg. Each day I found these eggs in their regular position in the nest. After that the parents sat on the five

eggs during three days, but on the third day the abnormal egg disappeared. I looked everywhere to learn the fate of the painted egg, but could not find anything. The parents continued the incubation of the remaining eggs.

IV. In the same nest, at the end of the incubation period, when two eggs were hatched, I took one of the two remaining and colored it also with eosin. My idea was to force the mother to see this red egg during the operations connected with the hatching. This egg was not removed but was hatched like all the others.

V. At the time of the second nesting, at the end of spring, I noticed a warbler building its nest in a bush at a height of about three yards from the ground. There were no screening branches around the nest and it was on a bough which hung forward, so that I needed a ladder to reach it. When the first egg was laid I took it, pricked it at both ends with a needle, emptied all the contents and put it again in the nest. The following day a second egg had been laid and I emptied it in the same way as the first. But unfortunately, when I came to replace it in the nest, the mother was looking from a neighboring branch at a distance of about three yards. While I was on the ladder, with my right hand in the nest and holding the branch with my left, she came and hovered for two or three seconds at a distance of about one foot. Then she flew away. Nevertheless she came again the day after to lay her third egg. I emptied the latter also. Then I wondered if she would refuse these emptied shells or continue brooding. But after the third day the mother left her nest and I did not see her any more.

VI. A blackbird was sitting on her eggs in a nest on the side of a road at the base of a bush, at a height of about one yard from the ground. I came slowly from behind and tried abruptly to seize the bird. She flew away crying harshly and abandoned her nest.

VII. The courage of the warblers which had triumphed over three preceding trials had again to be put to the test. Right after the hatching of the eggs, before the feathers had developed, I colored one of the fledglings bright green with water color. Despite its extraordinary appearance, its parents nourished it in the same way as the others.

VIII. The day after the hatching of the eggs of a sparrow I put into the nest, which was built in the roof of a house, a large

fledgling of another nest, which was about ready to leave it. It was so big that it covered all the others like a mother bird warming her little ones; nothing could be seen of the legitimate proprietors of the nest. I lay flat on the floor of the attic, at a distance of two feet from the nest, so as to observe what would happen. The attic was in semi-darkness, and the birds, coming from full light when bringing food to their little ones, could not see me. I stayed there for three hours and I saw the mother and sometimes the father coming on an average every twenty minutes and bringing food to this big intruder, into whose throat everything was stuffed. The parents did not notice that their own offspring remained underneath and got no food. At last I restored every bird to its right place.

IX. Here is the last tribulation I inflicted on the little and sympathetic family of warblers. I captured a lizard and fastened it by a running knot under the forelegs, in order to keep it near the nest. I was close by observing what the parents would do. But before the arrival of the mother, the lizard had already attacked one of the little ones. As I was there to maintain order I interfered and hung the lizard above the nest in such a way that it could easily be noticed by the parents and could not attack the little ones. There was a distance of about three inches between its tail and the nest. Hanging thus, the lizard moved now and then, but rather rarely because of the cold weather. The mother warbler came with something in her bill, looked at the lizard, turned aside at a distance of about half a yard, came again very near to the nest, flew away once more as far as she was at first and then stationed herself at about eight inches from the nest, looking at it. She remained for exactly ten minutes (by my watch) in this position, without making any movement. The little ones, during that time, were crying for food, and the lizard, whose position obliged it to look up, was swinging and twisting its tail and legs. After that the warbler approached and gave food to her little ones, and from that time she nourished them without paying attention to the lizard.

Conclusions

I. A great and sudden fright inflicted on a blackbird and causing her to cry has been sufficient to make her abandon her nest.

II. A fright, not too sudden yet strong enough to keep a warbler motionless during ten minutes, as that produced by the

presence of a lizard near the nest, has proved itself less effective. (I must note that this case is not adequately comparable to the preceding one; in the former case the nest contained eggs; in the present it contained fledglings.)

III. Numerous and repeated disturbances during incubation have never discouraged the birds.

IV. The blindness of the maternal instincts, well known in certain cases, as the brooding of the cuckoo's egg by another bird or the brooding of hen's eggs by other hens, has been confirmed by the fact that a mother bird (*a*) does not recognize a great difference of size in the eggs; (*b*) is not struck by a considerable difference of color either in the eggs or in the little ones; (*c*) does not know how to discriminate easily between a true egg and an empty shell; (*d*) brings food to a fledgling which has no kind of resemblance to her own little ones and forgets the latter. The last fact proves such a great blindness that it induces one to consider the movements of food bringing in the said case, as being akin, to some extent, to purely mechanical movements. It would be interesting to learn whether a mother sparrow would bring food to a mechanical puppet mimicking a fledgling.

V. A bird seems, according to my experiments, not to have a well-developed knowledge of the specification of the different kinds of dangers caused by the different kinds of enemies. When I chased the parents sixteen times from their nests, they behaved in the same way as if they were obliged to go out because of a strong shower of rain, for example, or because of the necessity of feeding themselves. A lizard near their nest seems to have frightened them in the same way as any other kind of unusual moving object. The cessation of movement or the acquaintance of the animal with it determines the cessation of fright.[1]

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[1] I express my gratitude to Professor A. Petrunkevitch for his valuable suggestions.